THE
AMERICAN NATURALIST

VOL. LI. *January, 1917* No. 601

THE PERSONALITY, HEREDITY AND WORK OF CHARLES OTIS WHITMAN, 1843–1910

DR. CHARLES B. DAVENPORT
COLD SPRING HARBOR

AT Pinhook, in the town of Woodstock, Maine, was born December 12, 1843,[1] a male child named by his parents, Joseph and Marcia Whitman, *Charles Otis*. Some time thereafter the parents and their children removed to Waterford (where they were in the '50s) and in 1861 to Bryant's Pond (Fig. 1). All of these places are in the southern part of Oxford County, 50 miles or so from the coast at Portland, in about the latitude of the Presidential Range of the White Mountains—a country of high hills and small mountains, covered with pine and hardwood forests, abounding in lakes with some fertile plains between; a country affording a stimulating environment to a boy with an inherent love of nature. And a love of nature was widespread in the boys of this country and in their fathers. Take, for example, Jacob Whitman. Born in Easton, Mass., twenty miles south of Boston and ten miles north of Taunton it would appear that his lines had been pleasantly cast. But[2] he had an adventurous spirit and was perhaps "very wilful." He was with the "min-

[1] The date is given as December 14, 1842, by Lillie, 1911, and Morse, 1912; also National Cyclopedia of American Biography, XI, p. 73. The date given above is that of the Whitman Genealogy. It also agrees with that remembered by Mrs. H. D. Smith (Mary Whitman) because her sister Sarah was born September 10, 1843, and Charles O. was born the December following.

[2] Cole and Whitman, 1915, p. 42.

55183

ute men'' in 1775, probably fought at Bunker Hill, was at Harlem Heights, stormed Stony Point, helped capture Saratoga, and was at Trenton. He had married, 1777, and, after the war, 1781, came to the frontier settlement of Buckfield, Maine, which had been settled some four years before. Fellow townsmen, by the name of Record,

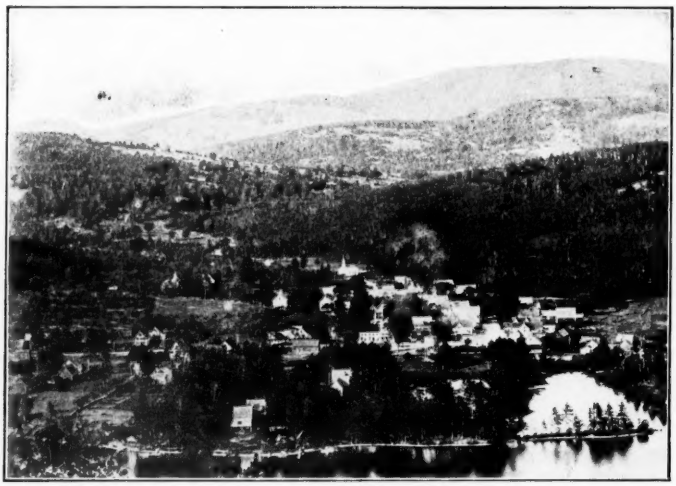


FIG. 1. View of village of Bryant Pond, Woodstock, Maine, home of Charles O. Whitman during early manhood. Note the church in the center, the school house with a bell tower to the left of the church and more toward the foreground. The Whitman homestead lies to the right of the school house, partly screened by trees. The pond is in the foreground and is backed, as seen from the village, by a lofty cliff from which the photograph was taken. Over these hills and through the pine and hardwood forests the young naturalist, Whitman, hunted. (Contributed by Professor Whitman's sister, Mrs. E. B. Reynolds, of Lynn, Mass.)

had previously settled there and had told Jacob Whitman about the town and their tales of conditions at Buckfield evidently appealed to him, and induced him to migrate thither.

He was a stout and muscularly built man . . . and was inured to hardship. . . . He was an industrious citizen and paid strict attention to the clearing up of his lot, rearing a family and attaining a competence. He was often selected for road surveyor, school agent, and school committee and his name was always kept in the jury box until he got too old to attend to such service. He was a man of fierce spirit when aroused and positive in his opinions and fond of argument.

He declined to join the first church started at Buckfield as he did not believe its creed. Of other founders and early settlers of Buckfield it is known that they were hunters and were attracted to the locality by observations made on hunting expeditions. Such were Nathaniel Buck "a man of great physical strength and endurance, and noted for being an expert hunter and skilled in woodcraft"; Thomas Allen, a deserter from the English army to the side of the colonists, a man of adventurous disposition, fiery temper and obstinate in his opinions; and Benjamin Spaulding who had retired from Chelmsford, near Lowell, Mass., to this wilderness, partly to avoid certain financial obligations and partly to trap and hunt.[3] Oxford County was, indeed, as much a frontier of civilization at the end of the eighteenth century as the Rocky Mountains were fifty years later and attracted much the same sort of adventurers, lovers of untouched nature, the forests and wild animals. It was the sort of blood from which naturalists might be expected to arise, and from Oxford County and from the adjacent counties of Cumberland and York have arisen such men as A. E. Verrill, of Greenwood, H. C. Bumpus, of Buckfield, and C. O. Whitman, of Woodstock (Oxford Co.); E. S. Morse, of Portland; A. S. Packard, of Brunswick (Cumberland Co.); Geo. B. Emerson, of Wells, and Geo. L. Goodale, of Saco (York Co.); and Elliot Coues from just over the boundary at Portsmouth, N. H.

Charles Otis Whitman was born December 12, 1843, in Woodstock, Me. As a boy he attended the town schools at Woodstock and Waterford, and worked on the home place. During the summers of 1857 and 1858, while at Waterford, he helped his father's brother, Elhanan, on the farm, as Elhanan's daughter, Mrs. H. D. Smith, of Norway, Maine, recalls very well. He was a good-natured boy and good company to his cousins. His cousin can not recall that he was engrossed in birds at that time; but by 1860 he had made a considerable collection which

[3] Cole and Whitman, 1915, pp. 24–5.

FIG. 2

FIG. 3

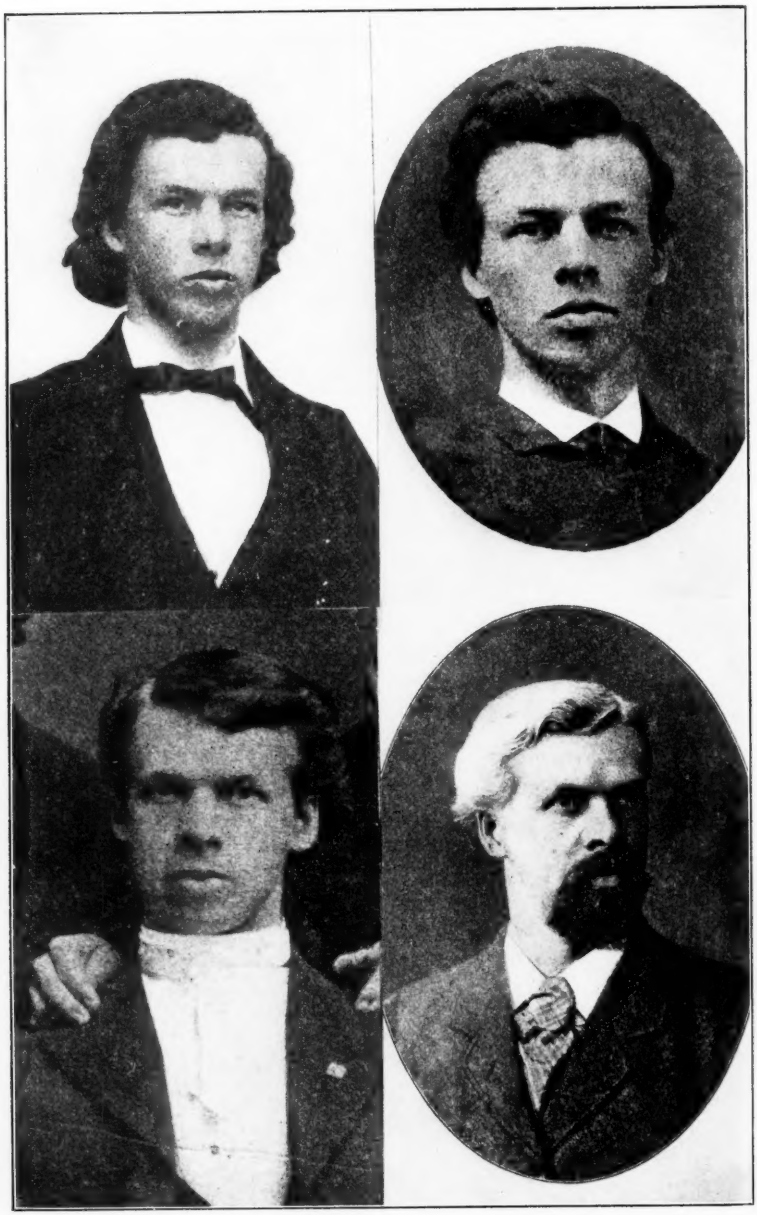


FIG. 4

FIG. 5

FIG. 2. Charles O. Whitman, at the age of eighteen years. This picture shows a great resemblance to his son, Carroll Whitman, at the time he entered Cornell University. From a tintype contributed by Mrs. E. B. Reynolds (Myra Whitman).

FIG. 3. Charles O. Whitman at the age of about twenty-one years. Reproduced from Lillie, 1911; where it is labeled, "1857, enlargement from a tintype. Kindness of Professor E. B. Morse." This would place the age at fourteen years. His cousin Mrs. H. D. Smith assures me that the correct age is as stated.

FIG. 4. Charles O. Whitman at the age of twenty-five years. This is one of a group and is probably of his class at graduation from Bowdoin College. (Note the "class pin.") Some of the other members of the group are full-bearded young men. From a silver print contributed by his sister, Adrianna Whitman Evans of Lynn.

FIG. 5. Charles O. Whitman at about thirty-nine years.

FIG. 6

FIG. 7

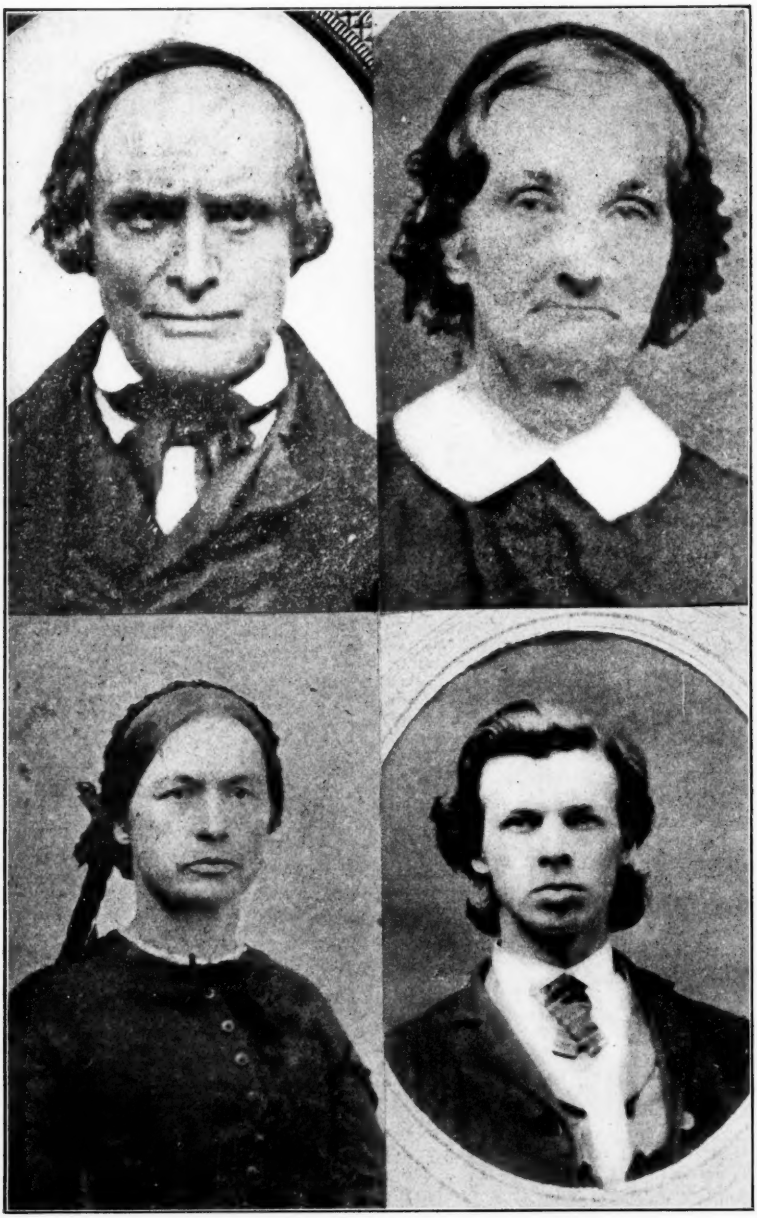


FIG. 8

FIG. 9

FIG. 6. Solomon Leonard, the father of C. O. Whitman's mother, from a daguerreotype in the possession of Mrs. Myra Whitman Reynolds.

FIG. 7. Esther French, wife of Solomon Leonard and mother of C. O. Whitman's mother. From a daguerreotype in the possession of Mrs. Reynolds.

FIG. 8. Marcia Leonard, wife of Joseph Whitman and mother of C. O. Whitman. Note the thick lower lip and slightly raised tip of nose. From a photographic print; kindness of Mrs. Reynolds.

FIG. 9. Charles O. Whitman, at about twenty years, for comparison with his mother. Note the restricted broad lip and the slightly raised tip of nose. From a tintype; kindness of Mrs. Smith.

FIG. 10

FIG. 11

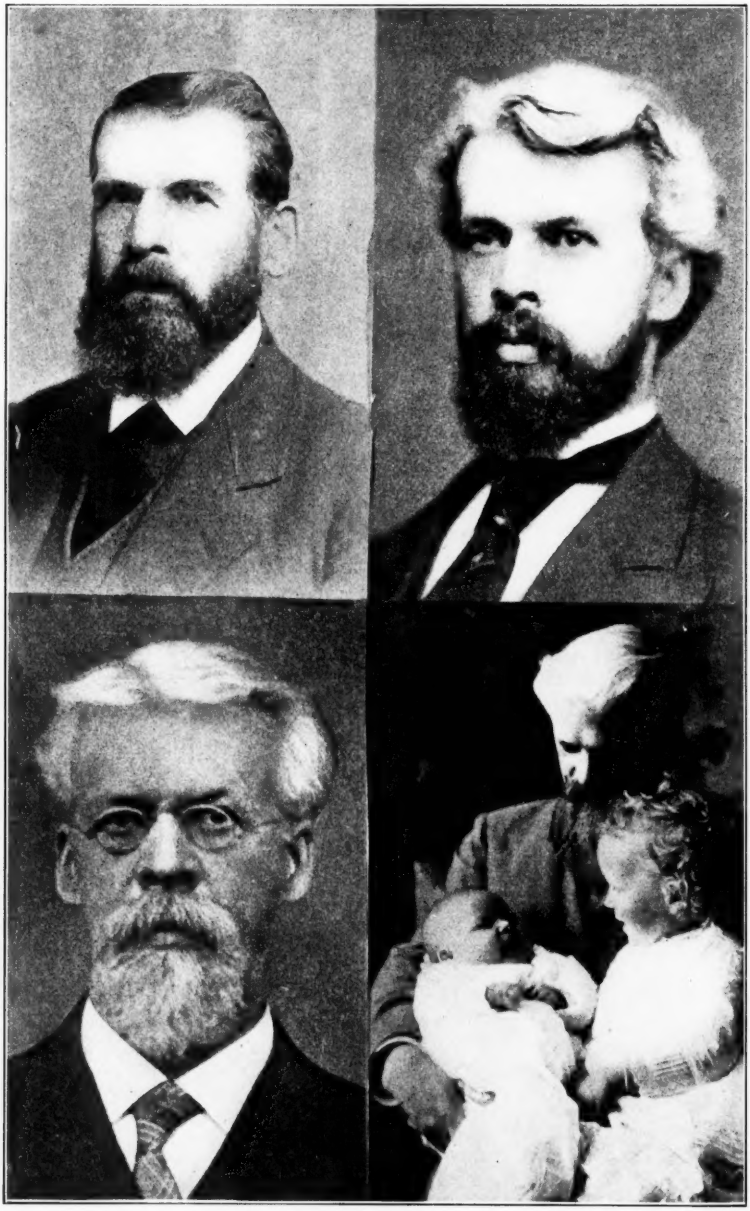


FIG. 12

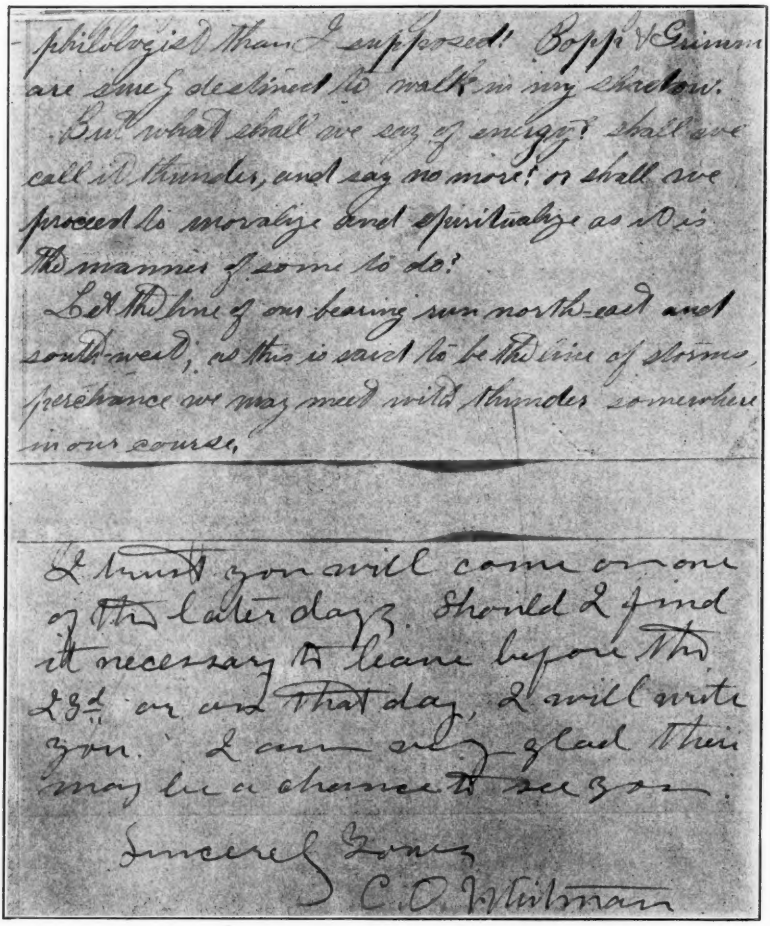
FIG. 13

FIG. 10. Joseph Whitman (2d), father of Charles O. Whitman. Note the wide nostrils, long tip of nose and wavy hair, turning gray.

FIG. 11. Charles O. Whitman, probably on his return from Germany, about 1878, age thirty-five years. The hair of the head is now quite gray.

FIG. 12. Charles O. Whitman, professor at University of Chicago, probably spring of 1900. Age 56.

FIG. 13. "The Father," about 1887.


philologied than I supposed! Bopp & Grimm are like destined to walk in my shadow.

But what shall we say of energy? shall we call it thunder, and say no more? or shall we proceed to moralize and spiritualize as D is the manner of some to do?

Let the line of our bearing run north-east and south-west; as this is said to be the line of storms, perchance we may meet with thunder somewhere in our course.

I trust you will come on one of the later days. Should I find it necessary to leave before the 23d or on that day, I will write you. I am only glad there may be a chance to see you.

Sincerely Yours
C. O. Whitman

FIG. 14. Handwriting of C. O. Whitman. Above, at Westbury Academy at about the age of twenty-six years. Below, at fifty-six years.

he had mounted in two great glass cases, nearly covering one side of the room. Lapham (1882, p. 166) says:

> So artistically prepared were they, and so naturally mounted, that they attracted much attention among ornithological students.

It is said that he was dissuaded from volunteering for the Civil War by his father's opposition; was drafted but re-

jected after examination. In the autumns of 1861, '62 and '63 and in the spring of 1864 Charles attended the Norway "Liberal Institute," an academy of high school grade, where his uncle, George F. Leonard, taught. It is said that he taught winters to obtain the means for paying his school expenses.

He entered Bowdoin College as a sophomore in September, 1865, and was given the degree of B.A. in July, 1868. Lillie attributes Whitman's strong views in favor of the requirement of Latin for a college education to the emphasis laid in his day on the classics at Bowdoin. He participated in the student literary and debating interests. He ranked about ninth in a class of 23, his rank having been decreased through the necessity he was under of teaching to earn funds for his college expenses. The following autumn he was appointed principal of the Academy at Westford, Massachusetts, and continued in this capacity until the spring of 1872. Here he apparently taught a variety of subjects. In September, 1872, he was appointed sub-master at the English High School in Boston where his uncle, George F. Leonard, had been for some years master. Here he taught general high school subjects until the summer of 1875. Morse states that he distinguished himself there by his original methods in teaching certain branches of elementary science.

"While in Boston," says Lillie, "Whitman came under the influence of Louis Agassiz and was one of the 50 students who, in July and August, 1873, attended the Anderson School of Natural History founded by Agassiz on the island of Penikese." Here he met Professor E. S. Morse, one of the instructors, who became interested in him because of his drawings, superior even to Morse's own. Whitman returned to Penikese in the summer of 1874, after which the laboratory was abandoned. The short-lived Penikese laboratory greatly impressed those who attended it and several of these became founders of other marine laboratories—thus, Hyatt of a laboratory at Annisquam, Whitman of one at Woods Hole, Franklin W. Hooper of one at Cold Spring Harbor, David Starr Jor-

dan of one on the Pacific coast at Pacific Grove, California. It was at Penikese, says Morse, that Whitman seriously began his life work in science, for shortly afterwards he went to Dr. Dohrn's laboratory at Naples and then to Leipzig where, under the great Leuckart, he learned methods of microtome section-cutting, staining of tissues, and processes of preparation far ahead of those used at Penikese; in short the modern methods of the embryologist and morphologist." He was in Germany for three years, being on leave of absence all this time from the Boston high school. In 1878, at the mature age of thirty-five, he received the degree of doctor of philosophy from the University of Leipzig and in the same year appeared his doctor's thesis, "The Embryology of Clepsine," in the *Quarterly Journal of Microscopical Science.* This paper of 100 pages introduced important new principles, as well as facts, into embryological science and was beautifully illustrated by his own drawings.

On his return to America Whitman took up again his work at the Boston high school, teaching English; but at the end of the year he had decided to become a zoologist, applied for and received a fellowship in biology at Johns Hopkins University and resigned from the English high school. But during the summer of 1879 he received an invitation from Professor Morse, who had been teaching zoology at the Imperial University in Japan, to fill his place. Accordingly Whitman set sail for Yokohama, August 21, 1879, and taught at Tokyo until the summer of 1881. Here he trained four investigators who all became professors of zoology in the university: consequently he may properly be called the father of zoology in Japan. He and the administration of the university became estranged, as he would not adapt himself to what seemed to him a desire for official control of intellectual property; also he felt that his work was insufficiently supported. As he left he published a somewhat harsh brochure entitled "Zoology in the University of Tokyo." Leaving Japan in August, 1881, Whitman worked at the Zoological Station of Naples as a guest of Professor

Dohrn, November, 1881, to May, 1882. He was interested in, and recorded, the methods of microscopical research at that station, and published an important paper on the embryology, life-history and classification of Dicyemids, which had some time earlier but, as Whitman proved, without warrant been elevated to the position of a subkingdom of animals, the Mesozoa.

Returning to America in the autumn of 1882 he was appointed assistant in zoology at the museum of comparative zoology of Harvard University. While here he worked in cooperation with Alexander Agassiz on the development of pelagic fish eggs. Two papers were published on this matter and plates prepared, but no text, for another. At this time he published his book on "Methods of Research in Microscopical Anatomy and Embryology."

In 1886 Whitman was invited to take charge of a private laboratory for biological and related research that Edward Phelps Allis, Jr., had planned to found on the Lake at Milwaukee, Wisconsin. With Allis's cooperation Whitman then started the *Journal of Morphology,* the first of its kind in America and based on such high ideals of quality and of beauty of plates that the eighteen volumes published entailed considerable financial loss, so that finally it had to be discontinued—although it was revived, after a lapse of five years, under other auspices. The three years, '86–'89, at the Lake Laboratory saw the beginning of some researches by Whitman, which were mostly never completed, and by his associates, Howard Ayers, William Patten, A. C. Eyeleshymer, as well by the founder of the laboratory. Some of the published work is of the finest quality.

In 1888 the Marine Biological Laboratory at Woods Hole was organized by certain residents of Boston and Professor Whitman accepted their invitation to become its director. It was in the development of this laboratory that Whitman's greatest work for science was done. For he introduced and upheld ideals of cooperation and scientific democracy which led to its loyal and devoted support by a large body of the working biologists of the country.

In the year 1897 a disagreement occurred between Whitman and a minor, but influential, portion of the trustees. The latter regarded him as extravagant, while he thought they hampered the proper development and organization of the laboratory. Some of the Boston supporters of the laboratory thereupon withdrew from the board; however, the development of the laboratory suffered no serious interruption. At the end of twenty-one years as director Whitman was led to resign, owing to the growing demands upon his time of his researches.

It was in the early years of the Marine Biological Laboratory that Whitman and some of his co-workers saw the need of a technical zoological society and a call for such a society was made by a committee of which he was chairman. He served as president for the first four years. At first known as the American Morphological Society, it has been known since 1902 as "The American Society of Zoologists," and is still the national society for this science.

In 1889, Clark University having been organized exclusively for graduate and research work, Whitman was called from Milwaukee to become its professor of zoology. He now took up again his work as a teacher which continued to his death. There gathered about him at Worcester, Massachusetts, a small body of devoted zoological investigators. What with the *Journal of Morphology,* the Marine Laboratory and the organization of the new department his time was pretty well filled. He published three short papers on the leech, *Clepsine.* But affairs at Clark were not altogether to his liking and when a call to the University of Chicago came in 1892 Whitman and the heads of the departments of physics, chemistry, anatomy, neurology and paleontology seceded from Clark University and formed the major portion of the scientific faculty of the new university. Here at Chicago Whitman had more graduate students than ever before, but as his research grew more engrossing he kept more and more to his home where his experiments were conducted. For a period of fifteen years he bred pigeons to get at an under-

standing of the evolution of their color markings. He usually had about 500 individuals, representing about 40 wild species, in dovecotes surrounding his house. He hybridized nearly 40 species, most of which had never been crossed before. His work included the phylogeny of pigeons, instinct and animal behavior, voice, fertility and the nature of sex.

Professor Whitman suffered considerably from indigestion for some years before his death. He contracted a heavy cold while caring for his pigeons and died suddenly, December 6, 1910, at the age of 67, of pneumonia, the same disease that his mother died of at the age of 57.

We have now to consider some of the personal characteristics of Charles O. Whitman, and their distribution in his family.

First, white hair. Charles Whitman's hair turned white unusually early. Morse quotes Judge Clarence Hale of Portland as saying that his hair was perfectly white when in college but his class portrait (Fig. 4) shows his hair still dark. At the age of 39 (Fig. 5) the hair is quite white. His father's hair turned gray early; Charles's brother at 49 has very gray hair. Early graying is apparently a "Whitman trait."

2. Wave in hair is shown by his father (Fig. 10) and as a dominant trait is doubtless inherited from this side.

3. Nostril. His father had broad nostrils (Fig. 10), but the ridge is carried apically beyond the level of the nostril. In Charles, as in his mother (Fig. 8), the apical knob was lacking, hence the nostrils appeared unusually full.

4. The lower lip is thick, especially near the median plane. His mother's portrait (Fig. 8) shows an exceptionally broad lower lip and this is exactly reproduced in her daughter, Adrianna. The mother's father (Fig. 6) also has a broad lower lip. Charles gets the breadth of lower lip from his mother's side and its restriction to the middle of this lip (Fig. 9) is doubtless due to another factor.

5. The forehead is broad and full (Fig. 12); doubtless a

Whitman trait, as it is strikingly reproduced in his cousin, Mrs. Smith. Moreover his grandfather Leonard had an exceptionally fine head (Fig. 7).

6. The general slenderness of form is a Leonard trait. His father and some of his sibs were stout, as is one of his sisters, while his other sibs are slender, like himself.

Taste for Natural History.—This was, doubtless, innate and it was very strong, developed very early, as we have seen above, and led to his keeping animals and mounting birds. Thus he kept, as a small boy, mud turtles, rabbits, guinea pigs, woodchucks, and raccoons. Later, his sister recalls, he kept two gray squirrels which were so tame that they would go to sleep in his pockets. He kept doves, which he would tend carefully and of which he would watch the young after they were hatched. These doves would cover him as he fed them. He was fond of hunting. His stuffed eagle was especially famous. On one occasion, at the age of twenty-four years, he was gone two nights and a day after an owl. Mr. H. T. Libbey, of Bryant's Pond, told me that on one occasion he went out with Charles after a large bird and was gone all day. It is interesting that the special objects of interest of his early years should have been those of his late years. If we seek for the origin of this strong taste in such an out-of-the-way part of the world we find it, as stated above, in the blood of the pioneer, adventurer, hunter and lover of nature which sought the wilderness of Maine at the end of the eighteenth century. Actually, one finds evidence of love of hunting and of nature in close relatives, especially on the father's side. First, Charles's sister, Adrianna, was as fond of natural history as himself. She had a tame bluejay which stayed about the house like a crow. Charles's uncle, Chauncey C. Whitman, was a farmer who devoted himself, in his later years, particularly to the *raising of horses and cattle.* It is told of him[4] that, when he was twenty-four, he joined his fellow townsmen on a bear hunt and finally the bear was found in his den under the roots of a large tree. Chauncey "had the temerity to

[4] Lapham, 1882.

thrust in his arm and catch hold of her hair, when she quickly turned and came out before them all." She had two cubs. One was *taken out alive and kept for several months* by Chauncey Whitman until, having become mischievous, it was killed. Here we see the same love of wild animals that Charles showed. This Chauncey had a son, Albert, who is a hunter living in Oxford County. He keeps squirrels, woodchucks, and other pets. Albert's brother, Thomas, had a *poultry farm* and his son still carries on the business. Charles's father's father, Joseph Whitman, father of Chauncey, was also a hunter and told his grandchildren hunting stories, including adventures with bears and other animals, which are keenly remembered to this day. It appears that the mother's father, Solomon Leonard, had a love of nature and took pleasure in his trout brook. So Charles got his love of nature from both sides of the house.

Scholarship.—But Charles had more than a love of nature; he desired to *study* nature. This scholarship is a family trait and comes to him from both sides of the house. It is noteworthy that in Lapham's "History of Woodstock, Me.," 1882, p. 56, it is stated:

> Three Woodstock men have graduated from college, George F. Leonard, Harrison S. Whitman and Charles O. Whitman.

The first is an uncle and the second a cousin of the third. According to Cole and Whitman (1915, p. 707):

> Judge Mitchell's "History of Bridgewater" says that more persons of this (Whitman) name in that town in early times received a college education than any other. The next most numerous were Packards.

And Charles's father's father's mother was Abigail Packard. It is worth while to consider in detail the direction taken by the scholarship of the close relatives of Charles. First, the mother's father, Solomon Leonard, was a close student of ancient history. But it was to the influence of his mother's brother, George F. Leonard, that the direction of Charles's early life was chiefly due. George Leonard graduated from Dartmouth with the class of 1859.

> He adopted teaching as his profession and instructed in the academies in Norway and Paris, in Maine, and in Northbridge, Mass. He was

also a teacher in the English high school in Boston, following this occupation for over twenty years. . . . He is a profound scholar and succeeded well in his teaching.

It will be noted that Leonard was teaching at the English high school, 1862–'82, at the time Charles O. Whitman was there and had preceded him there probably ten years. Leonard was especially interested in mathematics and during the later years of his life devoted much time to "squaring the circle," *i. e.*, to determining if the relation π can be exactly expressed by a fraction. He is said to have worked out the decimal to over 1,250 places. Relatives say that George Leonard helped secure a college education for Charles and his influence must have been great in getting his parents to let Charles go instead of, as eldest son, helping his father with his business. Leonard graduated, 1859, and taught, probably 1859–'62, at the academy in Norway and that at Paris only a mile or two away; Charles studied at the Norway Academy, 1861–'64. George Leonard, as we have seen, was already a veteran at the English high when Charles came there to teach, retaining his connection with it for seven years, and during this entire period his uncle taught there.

Another instance of scholasticism in this family is that of Charles's first cousin, Rev. Harrison Spofford Whitman, who was born 1844, a year or two later than Charles. Harrison is the son of Harrison Whitman, who was a farmer, at one time captain of an infantry company of Woodstock that saw some service at the time when war was threatened over the boundary of Maine; he was also some time coroner of Oxford County, and died at the age of thirty-one years, leaving a widow and three children. Harrison, Jr., early showed remarkable aptitude in composition (as did his brother and sister); he wrote both prose and poetry; he was fond of study, graduated at Bowdoin in 1869, teaching school meanwhile to earn his tuition and expenses, was for two years principal of the Thomaston Academy, '69–'71; then taught mathematics and later classics at the Dean Academy, Franklin, Massachusetts, '71–'74; then he studied theology at Tufts Col-

lege, graduating 1877. He has ever since taken a leading position in the Universalist ministry of Maine, having been pastor at Augusta and being now at Portland, Maine. He is an able preacher and popular among his parishioners.

This brief account of close relatives who have been distinguished scholars makes it clear how Charles O. Whitman found it natural to follow a scholarly career.

Thoughtfulness and Classicism.—Not all scholars are of the same type. In one type (the hyperkinetic or romantic) there is a rich flow of brilliant ideas and a rapid passage from one subject of interest to another. In the other type (the hypokinetic or classic) there is a profundity of consideration of a subject and a persistence of interest in it. Charles O. Whitman belonged to the latter type. This type ordinarily shows a recessive inheritance. His mother apparently showed this type. She was gentle and pleasant and never lost her even temper; while in many of the Whitmans the temper was of the periodically explosive sort; but there is evidence of the classic temperament on the paternal side, *e. g.*, in Harrison S. Whitman.

That Charles Whitman was of the classic type and was thoughtful will be generally conceded; he was, indeed, one of the best examples of this type that one could find. He felt little pressure to express himself. His principal biographer (Lillie, 1911) records only 67 titles of which 7 are his annual reports,—reports that, toward the end of the series, were secured only with much difficulty and after long delay, and for the last twelve years not at all. Of the remaining 60 there are hardly 20 that are to be classed as typical professional papers, giving the final results of finished observation. Some of the papers are brief notices of technical methods (Methods in the Zoological Station in Naples, 1882, with a French translation; treatment of pelagic fish eggs, 1883; means of differentiating embryonic tissues, 1885; osmic acid and Merkel's fluid, 1886). Other papers are polemical (new facts

about the Hirudinea critique of Apathy, 1888; Apathy's grief and consolation, 1899).

A group of papers (9) of a semi-popular sort relate to the work and aims of the Biological Laboratory. Most of the remaining non-technical papers are delightful essays, chiefly upon philosophical biological matters. Such are: "The Seat of Formative and Regenerative Energy," 1887; "The Naturalist's Occupation," 1891; "The Inadequacy of the Cell Theory of Development," 1893; "General Physiology and Its Relation to Morphology," 1893; "Evolution and Epigenesis," 1895; "Bonnet's Theory of Evolution; a System of Negations"; also "The Palingenesia and the Germ Doctrine of Bonnet," 1895; "Animal Behavior," 1899; "Myths in Animal Psychology," 1899.

The more strictly investigational papers fall into three periods: (1) The invertebrate period—devoted chiefly to the leech, *Clepsine*, which was the subject of his doctor's thesis and upon which he wrote more or less from 1878 to 1899—a period of 21 years. Here also belongs his Naples work on Dicyemids. (2) The period of vertebrate embryology, beginning with work done with Alexander Agassiz on pelagic fish eggs, 1883–1889, on amphibian eggs, 1888, and the ganoid fish, *Amia*, 1896. (3) The period of genetics, foreshadowed in his note "Artificial Production of Variation in Types," 1892, and continued with the pigeons to the end, 1910, in all eighteen years. In his work with worms, amphibians and pigeons he was led to reflections upon animal psychology and to the publication of his classic paper on animal behavior, 1898, and his brief paper on myths in animal psychology, 1899.

Many of these papers are highly finished and give the results of prolonged contemplation. Professor Whitman, especially in his later years, repeatedly spoke disdainfully of rushing into print and making an annual "dump" of scientific gleanings—and these were the natural expressions of his own nature; perhaps he insufficiently recognized that all persons were not constituted like himself and could not react in the same way. Whit-

man, indeed, planned to publish far more than he did; he had accumulated materials that were nearly ready for the printer. But the absence of the hyperkinetic *drive* combined with the manifold duties of the moment led to procrastination for the more convenient period of prolonged quiet which an overactive world never afforded him. On the other hand, had it not been for the exceptional pressure brought to bear on him for an address or a contribution we might have had less than we have from his pen. Of his writings Lillie truly says (p. lxxiii):

> His published papers, mostly short, are models of condensed thought, written in a fine, polished, characteristic style. No less care was devoted to the form than to the substance, and some of his papers will certainly endure as classics of the biology of his time. . . . He rarely had occasion to correct any published statement, and even less rarely, perhaps, to change in any radical way a point of view to which he had once committed himself.

Conservatism, so frequently associated with hypokinesis, was marked in Whitman. He was not very cordial to developmental mechanics, and was critical of the enthusiastic rush to the mutation theory and Mendelism. He could not easily abandon old ideas for new, and ally himself with the latest biological fad.

A strong philosophic and argumentative tendency is found on both sides of the house. His mother's father was much given to theological discussion, and was an ardent adventist. Charles's father, too, was argumentative. The philosophic tendency in Whitman was marked in his writings. In one of his manuscripts of Westford days, at the age of 26, he discusses the topic "Progress Has No Goal" and again "Womanhood Suffrage," of which the tenor is shown by the concluding sentence:

> Female suffrage . . . may meet with opposition, as indeed, every reform does, but all this opposition is but the alarm of the great clock of human progress, which is soon to strike the hour when all enlightened nations shall recognize not only manhood but also womanhood suffrage.

This is quoted as an illustration of youthful style and not a statement of his views in later life.

Whitman's hypokinesis shows itself even in his handwriting. It altogether lacks the running dash of the

hyperkinetic. Each word is worked out with some effort. It is interesting to compare his chirography of Westford Academy days (when he was about twenty-six) and that when he was fifty-six (Fig. 14). There is the same loop from the end of the word to cross the "t" in "the"; the same scanting of the terminal "y"; the same form of the capital "I." In thirty and indeed in the course of forty years his handwriting showed no important change.

Deliberateness.—Professor Whitman's movements and speech were characterized by deliberateness—another characteristic of the classical type. It is, of course, a mere caricature to say, as an unkind critic once did, that his lectures consisted of pauses punctuated by sentences. I mention this because it brings vividly to mind a way he had in lecturing or addressing his seminar students to pause frequently for some seconds looking pleasantly over the room before beginning the next sentence. Even in conversation he would turn a calm, thoughtful face toward you and express himself clearly and deliberately. So marked a deliberateness is not shown by his sibs, but his brother shows something of it, and I am told that his father was slow of speech.

Literary Ability.—While Whitman did not have a strong internal impulse to write, what he published is mostly characterized by high literary finish. Speaking of cooperation between the organic and the inorganic sciences he says (1895, p. iv):

> Comparison of standpoints must benefit both sides. Cross fertilization works rejuvenation in theories as in organisms. The biologist may pause to see how the individual vanishes in the abyss of the universal, and how self determination dissolves in the pressure of the physicist's fundamental postulate of inertia. The physicist may find it agreeable from time to time to turn from the Nirvana where self and not self, rocked in blissful reciprocity of vibration, annul each other, to the world where self asserts itself in organic determinations, issuing in purposeful adaptations and conscious, intelligent action.

Again, speaking of Bonnet he says:

> With a zeal never daunted, and an ingenuity seldom baffled, never defeated, he piled mountain upon mountain of negation, rolling Ossa upon Olympus and Pelia upon Ossa, until the whole organic world

seemed to be completely buried under a stupendous mass of negations, blinding in one infinite negation—*No Change.*

Perhaps something of Whitman's interesting and vivid style may be referred to the influence of his teaching of English in the high school; but much of it appears in papers written before the Boston days. In them, too, he frequently uses the rhetorical question so often found in his later writings (cf. Fig. 14, upper). I think we must conclude that this literary ability has a constitutional basis. We have seen above that his cousins, children of Harrison Whitman, "early showed a remarkable aptitude for composition both in prose and poetry." A granddaughter of Chauncey Whitman, brother of Charles's father, was an authoress of poetry, for which she found a market.

Pertinacity.—In Whitman's combination of traits was found an element of pertinacity that was at times very formidable. Had it been less he could hardly have successfully overcome the handicap of comparative poverty, despite which he went through college. It showed itself again when he insisted in Japan that his student's papers should be published under their own names: and, when, since he was overruled, he resigned his professorship. It showed itself again in his struggle with a minority of the trustees of the Biological Laboratory, in which his views prevailed. It showed itself still again in his relations with Clark University, which led to his acceptance of the offer to go to Chicago. In minor departmental and laboratory affairs, as his colleagues well recall, this gentle-mannered man would show at times uncommon resistance to suggestion and persuasion. One, therefore, learns with interest that his father also was set in his opinions and could not readily be made to change his views. Indeed, Charles is seen to be an interesting mixture of gentleness, as shown also by his mother, and tenacity of purpose, as shown also by his father, his mother's father and other members of the family. Closely akin to his insistence on his ideals was his uncompromising disposition. As Lillie well remarks,

> It is questionable whether his life would have been so valuable, had his disposition been more pliable.

One other trait that sometimes showed itself, especially in his writings, was his capacity for trenchant and satirical criticism. Morse (1912, p. 283) has given some examples. It is characteristic of many hypokinetics to feel deeply and to resent warmly. In weighing any criticism we must always consider the personality of the critic. Perhaps in this reaction of Whitman's we see trace of a Whitman "sternness" shown also by his father.

Artistic Taste.—Professor Whitman had a keen artistic sense. This is proved by the success, in his boyhood, of his mounts of birds. I think we may go back of this and find evidence of an artistic sense in the appeal made to him by natural beauty—the beauty of forests, flowers, birds and beasts. To a person without the sense of beauty natural forms have little attraction. Later this sensitiveness to and love of form shows itself in the beautiful drawings he made at Penikese, the exquisite plates of leeches and the delicate pencil drawings of the Dicyemids. It is clear that the art of Japan appealed strongly to him and he had in his house at Chicago many examples of that art. It was love of form that made him a *morphologist* and led him in the *Journal of Morphology* to introduce a beauty of execution of plates exceeding anything then current in America. It was this sense of beauty that led him to select excellent Japanese artists to draw and paint his pigeons. While I have not been able to make an exhaustive study of the distribution of artistic sense in his relatives, it appears that his father, who was a carriage manufacturer, was an artistic one. The woodwork of the finish was done very carefully, the wheels made by hand and so artistically was the whole executed that he once received a silver cup as prize for one of his carriages at a competitive exhibition. On the other side we find his mother's father, Solomon Leonard, was also an artisan. He established an iron foundry at Pinhook and his kitchen ware was so satisfactory that "the name of Solomon Leonard was known in every household." When later he retired from business he maintained "a small furnace at Bryant's Pond, where he made small castings to pass away the time." So it seems probable

that a taste for the beautiful in form and color had a constitutional basis in Charles.

Musical ability is frequent in the Whitman side of the house. Nearly all of the Whitmans could sing; especially good were his father's brothers. But Marcia Leonard, the mother, could not carry a tune; and the children were apparently not good singers. Charles tried to learn to play the melodeon when he was a boy, but had no aptitude for it; his elder sister, however, plays well on the piano and her son is a performer on the violin, of great ability, and a brother of Charles plays the violin well.

Of *mechanical ability* Dr. Whitman had more than the average man. His success in mounting birds (in his father's carriage shop) required manual dexterity. His sister recalls that he made a martin house. This ability shows itself again in his interest in methods of microscopical research which culminated in a volume—the only book he ever wrote—entitled: "Methods of Research in Microscopical Anatomy and Embryology," 255 pp., Boston, 1885. Of this book 55 pages are devoted to instruments and methods of imbedding, including 28 figures of machinery and apparatus, and pages of descriptions of the principles and details of this apparatus. It is improbable that Whitman would have collected such materials and written such a book had he not been interested in and had an insight into mechanical devices. This taste he maintained to the end, and he tarried long over a student who had invented some new instrument.[5] This mechanical insight enabled him to do things in ship-shape fashion. His charts and general arrangements of his laboratory and breeding pens showed this *savoir faire*. With less mechanical skill the feat of moving his pigeons to Woods Hole and back each year would hardly have been feasible. Whitman came from a race of artisans on both sides. His father was a carriage maker; his father's sister Loney had a son, Edwin, who is a machinist and another, Edson, who is overseer in a fabric mill. One of his uncle Cyprian Whitman's sons is an engineer. Of Elhanan Whitman's sons, Austin was a farmer with more

[5] Dr. Oscar Riddle.

than average mechanical ability and Edgar was a carpenter and always ingenious. Even Elhanan's daughter, Mary, says she is handy with tools and so are all of her sons. On the mother's side we have doubtless mechanical interests in at least the grandfather, Solomon Leonard, the iron founder.

The social instinct was highly developed in Whitman. While he rarely appeared at social functions and seemed to shrink from exercising the presidential office to which learned societies repeatedly elected him, yet he liked the society of his younger colleagues, frequently had informal lunches or dinners and, after the excellent meal, would encourage the guests to sit and talk on the matters that were uppermost in the minds of such young and ardent students of biology.

Given a young man of good health, fairly ambitious, dogged, scholarly, gentle, friendly, philosophical, conservative, with an ardent love of natural objects, literary and artistic ability of a high order, and with a *savoir faire* and place him in an environment of a scholarly uncle who is in a position to assist his nephew; of the stimulus of magnetically charged biological atmospheres at Penikese and at Leipzig; of an epoch when new machinery and new methods are being rapidly introduced into a new science; of a period in a young science that demanded organization of laboratories, university departments, societies and journals; and the reaction is that of the propositus; even though handicapped (?) with a hypokinetic temperament, an uncompromising attitude and, in his earlier years, an occasional tendency toward caustic criticism. At any rate such was the man, such the environment that provided the stimulus, and such the life history of Charles Otis Whitman.

LITERATURE CITED

Cole, Alfred and C. F. Whitman, 1915. A History of Buckfield, Oxford County, Maine. Buckfield, Me. 758 pp.

Farnam, C. H., 1889. Genealogy of Whitman Family.

Lapham, W. B., 1882. History of Woodstock, Maine.

Lillie, F. R., 1911. Charles Otis Whitman. *Journal of Morphology*, XXII, pp. xv–lxxvii. Dec.

Morse, E. S., 1912. Biographical Memoir of Charles Otis Whitman, 1812–1910. Nat. Acad. of Sci. Biographical Memoirs, Vol. VII, pp. 269–288.

MENDELIAN FACTOR DIFFERENCES VERSUS REACTION SYSTEM CONTRASTS IN HEREDITY[1]

T. H. GOODSPEED AND R. E. CLAUSEN

DURING recent years there has been a remarkable advance in our knowledge of Mendelian principles of heredity. This advance has for the most part had its source in the important and fundamental work of Morgan and his associates (1915) in which they have been concerned with the mutations of the common fruit fly, *Drosophila ampelophila*. The results of other work, in so far as agreement has permitted, have been brought into harmony with the principles arrived at through these investigations. As a result there has been developed a fairly clear and comprehensive conception of the constitution of the hereditary material and the nature of the mechanism by which it is distributed in gametogenesis, a conception which furnishes a consistent explanation of the products of Mendelian studies.

Morgan has stated that the fundamental principle of Mendelism may be reduced to this, that the units contributed by two parents separate in the germ cells of the offspring without having had any effect on each other. This conception of the absence of any factorial variability save that concerned in the discontinuous changes in factors involved in mutations has furnished the working hypothesis for Morgan's brilliant analysis of the germ plasm of *Drosophila*. Although the results of the *Drosophila* investigations have been ably presented elsewhere (Morgan et al., *l. c.*) it seems well briefly to review them here especially as they are vital to the argument presented in this paper.

[1] The investigations herein reported have been assisted by that portion of the Adam's fund granted to the department of botany by the department of agriculture of the University of California.

The large amount of data which Morgan and his associates have collected within the past six years has clearly demonstrated that the chromosome mechanism furnishes a basis upon which the behavior of Mendelian units may be logically and consistently explained. In an investigation of *Drosophila* over a hundred factor mutations have been discovered and studied, and these have been found to fall into four groups with respect to the linkage relations they display with one another. These four groups correspond to the four pairs of chromosomes. By determining the linkage values which are displayed within groups it has been possible to demonstrate that there is a consistent, invariable, linear arrangement of factors within the chromosomes at some time in their history. From this data Morgan and his associates have been able to prepare a map of the relative positions of the factors in the chromosomes. The complete conception, therefore, pictures the chromosome at some stage in its history as a linear series of loci. When a change occurs in some locus, a corresponding change of some sort may occur in somatogenesis, so that the individual which develops from such a set of factors with the changed locus differs in some particular way from an individual which develops from the normal unchanged series of loci. The change in the characters of the individual will depend not only upon the particular locus which has been changed, but also upon the particular way in which that locus has been changed. A changed locus, however, maintains the same position with reference to the other loci as did the unchanged locus, and this fact is the basis of Mendelian behavior, for knowing the behavior of the chromosomes in reduction, it enables us to gain a clear conception of the nature of Mendelian segregation.

When now we consider the particular factors themselves, the changed loci of the system, we see clearly that important physiological relations exist among the various loci. It is an appreciation of this fact that has led many investigators, among them Conklin (1908), Jennings (1914), Morgan (1915 *b*), Pearl (1915), and Wilson (1914),

to insist that the factors can not be regarded as determiners in themselves; but rather that they are differentiators, that working together with other factors in the system a difference is produced in somatogenesis which has its origin in some difference, some change in a locus in the system. For when in *Drosophila* a change in the locus *W* is produced, or in *Y*, such that the individuals developing from systems with these changed loci are white-eyed in the one case and yellow-bodied in the other, it seems evident that the change is more profound than the color of eyes or of body; that beyond these changes there is an underlying, elusive, physiological change resulting in individuals that are less vigorous and less fertile than those which develop from the normal unchanged system. The fact that a factor may have a primary, simple, easily recognizable effect and secondary far reaching effects, the latter to be attributed to the modified physiological relations resulting from a change in one of the members of a system, is one which has often been observed and which is of fundamental significance in our conception of the interrelations of the genetic factors. There are, however, other instances which may be cited of a somewhat similar nature, locus changes which produce certain characteristic effects under particular environmental conditions, but fail to disturb the normal behavior of the factor system when these conditions are not met.

It would, of course, be possible to recount almost indefinitely the specific effects of particular locus changes, whereas evidence concerning these far reaching effects of single factors is too scanty to warrant further discussion of this point. However, Morgan (1915 *a*) has been able to establish the relations displayed by the factor for abnormal abdomen and to demonstrate that only under very particular conditions is the presence of this genetic factor manifested by its characteristic expression, and that when these conditions are not present the product of somatogenesis may not differ in appearance from the normal fly, although differing from it both in genetic constitution and

hereditary behavior. We have thus a factor here which evidently has such a relation to the other members of the factor system that only under peculiar environmental conditions does it disturb the normal course of somatogenesis. Miles (1915) has likewise investigated a type of chlorophyll reduction in maize in which the recessive forms are yellow seedlings which usually show a distinct greenish tinge at the tips of the leaves. This type of chlorophyll reduction displays normal Mendelian behavior in inheritance giving in the progeny of heterozygous plants a ratio of approximately three seedlings which are of the normal green coloration to one which is of the yellowish type. The heterozygous plants possess the normal depth of coloration and can not be distinguished from those which are homozygous for the production of normal chlorophyll coloration. The yellow seedlings on the other hand form a distinct and easily recognizable class with no tendency toward intergradation, an observation which we have ourselves been able to confirm in independent mutations involving this locus. Usually these seedlings die as soon as the food material in the endosperm is exhausted, for under ordinary conditions the change in the locus is incompatible with a normal development of the individual, it is too profound an alteration to give a normally functioning factorial system. Miles found, however, that when the yellow seedlings were grown under particularly favorable conditions, they developed a normal chlorophyll coloration and produced plants which were able to go on through the cycle of changes included in the normal development of the maize plant. Now this behavior can not be referred to any change of the reduction locus back to the original condition, for the progeny of such plants consisted entirely of yellow seedlings; indeed, such a reversion would be inconceivable. Obviously the explanation of the situation will be found only through a consideration of the system with the recessive reduction locus. Normally this unchanged locus performs a definite function in determining the production of chlorophyll in the plant, but this function is

performed in conjunction with a number, perhaps a very great number or even all, of the other loci within the system. With a change in this particular locus, however, comes a change in the normal course of events in chlorophyll production, in that the rate at which the system is able to produce chlorophyll has been altered. Nevertheless, this change does not completely prevent the system under favorable conditions from going on and ultimately developing the same reaction end product which would have developed in the normal unchanged condition, but more rapidly.

Among such factors as have a profound influence upon the interrelations within the systems of which they are a part are those which Morgan (1914) has called lethals. Morgan's work with lethals is particularly suggestive because he has been able to demonstrate that they, like other normal Mendelian factors, occupy a definite locus in the chromatin system and display the same perfectly definite and consistent behavior with reference to the other loci of the system as do all other changed loci which do not interfere with the normal development of the individual. It is entirely possible that some of the lethals, like the chlorophyll reduction locus which we have discussed above, may yield systems which occasionally permit of the normal development of the individual, at least certain peculiar sex ratios which have been obtained might indicate that fact (Morgan, *l. c.*); but the important result of these investigations with lethal factors lies in that fact that certain kinds of changes in some loci are incompatible with normal functioning of the chromatin system. It might in addition be noted that there seems to be no particular reason why we should not include in the same category with lethals, the type of chlorophyll reduction mentioned above and those other types in maize which result from such profound factor changes that no development is possible after the food supply of the endosperm is exhausted.

Now giving the above results their broader and more general interpretation, it would appear that the factors

make up a reaction system the elements of which bear a more or less specific relationship to one another. It is this specific interrelation of the factors of the reaction system which determines that wheat produces wheat, and corn, corn, and so on through the whole realm of living matter. With this in mind it is at once apparent that normal Mendelian behavior can not be considered as a contrast of different reaction systems, but that in such cases the two organisms contrasted must possess fundamentally the same reaction systems, only a relatively few elements within the reaction system differing, and these not in a fundamental fashion. In fact it seems entirely logical in the light of modern Mendelian developments to consider each particular locus as made up of a definite nucleus, some complex organic compound perhaps, with a number of end chains which may be altered in various ways without changing the structure of the nucleus of the locus. According to this conception the fundamental relation of the locus to the other elements of the reaction system would remain unchanged, while the end product would be altered in some particular manner. There is probably no more striking confirmation of this conception than the suggestive hypothesis of multiple allelomorphs which Morgan and his associates (1915, *l. c.*) have developed. Their results and those of others in this connection seem to show clearly that the explanation of Mendelian differences on the basis of such a profound change as the dropping out of an element from a delicately balanced reaction system is practically out of the question. In multiple allelomorphs we have not one, but several, changes within the same locus. The similar effect which these changes have on certain organs of the body, for example, that relation shown in the locus *W* in *Drosophila* as a consequence of which the normal red eye color may be changed to white, eosin, or cherry depending upon a particular change in the locus, are such as to indicate that these are probably changes around the fringe of the molecule and not such as fundamentally affect the structure of the entire locus. Moreover, the relations thus exhibited again indicate that

the locus has a particular place and function in the reaction system, that it bears a specific relation to the other elements of the system.

It is true that investigation in plant breeding has not yet progressed far enough to furnish a definite confirmation all along the line of the work with *Drosophila*. The reasons for this are very obvious and they lie in the technical difficulties involved in such work rather than in fundamental disagreements in principle. It has not as yet been possible to study as many factors in any plant species as have been investigated in *Drosophila*, nor to carry the work through as many generations nor to employ as large populations. Moreover, most plant material is more difficult to handle from the standpoint of a chromosome analysis on account of the longer period of time necessary to secure data and the greater amount of attention which must be given the cultures and the larger number of chromosomes which are usually involved in such species. It must also be borne in mind that practically all the *Drosophila* differences have arisen under observation as simple factor mutations, and it has therefore been relatively easy to determine their relations to the other factors in the system. In plants, on the other hand, the material has presented itself as a confusing array of varieties containing for the most part a large number of recessive factors, and usually the original form from which they were derived, corresponding to the *normal* fly of Morgan's work, has not been obtainable and would not have been particularly useful, had it been available. Nevertheless, there appears to be no real difficulty in the way of accepting the conception derived from the *Drosophila* studies as a definite, consistent working hypothesis; for it is difficult to believe that the behavior of plant material should be fundamentally different, and indeed points of correspondence are not lacking to warrant us in viewing somewhat sceptically any undue emphasis placed upon the differences which may seem to obtain.

We may now return to the conception of the reaction system as a unit in itself in the sense that it is made up of

a large number of elements which bear a more or less specific relation to one another. This is the important physiological conception which has grown out of the vast amount of work which has been done in recent years in the analysis of the hereditary material. This is no new contention; it has been advanced and ably advocated by many investigators, but we feel that certain consequences of this conception have not been given the consideration their importance deserves. For if this conception be valid then it should not be possible, in certain cases at least, to shift and recombine the elements from which systems have been built up in the haphazard way that some advocates of Mendelism have attempted to do. If, for example, it is possible to obtain hybrids involving not a contrast between factors within a single system, but a contrast of systems all along the line, then it is obvious that we must consider the phenomenon on a higher plane, we must lift our point of consideration as it were from the units of the system to the systems as units in themselves.

Our attention has been called to this extension of the Mendelian conception by the behavior of species hybrids of *Nicotiana* which have been studied at the University of California during the past six years. This study has been concerned particularly with hybrids between *N. sylvestris* and varieties of *N. Tabacum*. These species, the former represented in the collections of the University of California Botanical Garden by a single type and the latter by a considerable variety of distinct forms, belong to entirely distinct sections of the genus *Nicotiana* and differ in important particulars which have been described elsewhere (Setchell, 1912). Goodspeed (1913) has studied a large number of different reciprocal hybrids between *sylvestris* and various of the distinct varieties of *Tabacum*. These hybrids are all partially sterile. It is possible to obtain a few viable seeds from open pollinated flowers and from those pollinated with *Tabacum* and *sylvestris*, but it has never been found possible to obtain any selfed seed. The phenomena displayed by these hybrids in development and inheritance admit of a consistent ex-

planation, if we regard them as the outcome of a contrast of two distinct Mendelian reaction systems the elements of which can not be freely interchanged without profoundly affecting the general functions of the reaction systems thereby resulting. We shall take up in very general fashion the points which have inclined us to this view, reserving for a later treatment the discussion of the hypothesis in detail and also the presentation of the extended data.

When hybrids are obtained between *sylvestris* and the various varieties of *Tabacum* they agree throughout in F_1 in presenting the entire set of characters of the *Tabacum* parent to the exclusion of those of *sylvestris*. This behavior may be definitely accounted for as a dominance of the *Tabacum* reaction system as such over the *sylvestris* reaction system. For point by point and character by character throughout, the correspondence between the *Tabacum* variety and its F_1 *sylvestris* hybrid may be demonstrated in a remarkable fashion and this irrespective of whether the factors concerned in these character expressions in the *Tabacum* varieties are dominant or recessive in varietal crosses. This correspondence is not only apparent in general appearance, but it extends to minute details of form and structure, and it is displayed even in the more intangible characteristics generally included under the term habit—*i. e.*, such characteristic varietal peculiarities of expression as the method of branching, insertion and inclination of the leaves, the type of inflorescence, and so on through a whole series of details. For example, when *N. Tabacum* var *macrophylla* (Setchell, *l. c.*, p. 8) is the *Tabacum* parent, the F_1 hybrids display the particular appearance and also the particular characteristics of *macrophylla*, except that throughout they are expressed on a very much enlarged scale (*cf.* East and Hayes, 1912). The broad clasping leaf of *macrophylla* with its distinctly pointed tip is faithfully reproduced in the hybrids. The flowers show no effect of the very much elongated corolla tube and the lobing of the limb peculiar to *sylvestris*, but display the *macrophylla*

proportions throughout. The stout tube, swollen infundibulum, and pentagonal limb are clearly derived from *macrophylla,* and the color is rose red of approximately the same depth and tone as that of *macrophylla* and in striking contrast to the pure white of *sylvestris.* In habit the hybrids resemble *macrophylla.* In early growth they are not characterized by the long maintained rosette which is so characteristic of *sylvestris,* and in leaf distribution, branching, and type of inflorescence they again correspond to their *macrophylla* parent.

When an entirely different set of characters is concerned in the *Tabacum* parent the F_1 hybrid with *sylvestris* is still an exact replica of the particular *Tabacum* used. For instance *N. angustifolia* (Setchell, *l. c.*, p. 9) and *sylvestris* give a hybrid which is entirely different in general appearance and all details from that obtained between *macrophylla* and *sylvestris,* and which displays throughout the *angustifolia* characters. The leaves of the hybrid are obliquely ovate-lanceolate and taper gradually to a long, curved point. They are also distinctly petioled like those of *angustifolia.* These characters are in striking contrast to those characteristic of the leaves of *sylvestris,* which are broad throughout, broadly pointed, and have a broad clasping base. When flower characters are examined, *angustifolia* is again faithfully reproduced in the F_1 hybrid for its flowers have the slender, straight corolla tube with practically no suggestion of an infundibulum and the deeply divided limb with narrow lobes that taper into long slender tips, all so characteristic of *angustifolia.* Like those of *angustifolia* the flowers are pink. In habit these hybrids again resemble *angustifolia.* This resemblance is displayed in a particularly striking fashion in the graceful, drooping manner in which the leaves are borne in marked contrast to the stiff, erect manner in which the leaves are borne by *sylvestris.* Throughout, *macrophylla* and *angustifolia* present a strikingly contrasted set of characters, yet in each case they are reproduced in their entirety in F_1 of the hybrid with *sylvestris.*

When particular tagged Mendelian factors are considered the same behavior is displayed. Perhaps there is no more striking instance of this than that shown by the expression of the calycine flower type in these *sylvestris* hybrids. When *N. Tabacum* var. *calycina* (Setchell, *l. c.*, p. 6) with its peculiar split, hose-in-hose flowers is crossed with *Tabacum* varieties of the normal flower type, the F_1 hybrids display the normal flower form and segregation occurs in F_2 into normal and calycine in accordance with simple Mendelian expectations. But when the *Tabacum* reaction system carries the recessive calycine flower factor into these species hybrids with *sylvestris* then every flower on the F_1 plants displays a more or less calycine structure. Similarly when the parthenocarpic characteristics of *N. Tabacum* var. "Cuba" (Goodspeed, 1915) are carried in by the *Tabacum* parent then the F_1 hybrid, instead of shedding its capsules soon after anthesis as is the case in all the other *Tabacum-sylvestris* hybrids, retains them indefinitely, in spite of the fact that no good pollen is produced, and thus non-fertilization, the stimulus for fruit abscission in *Nicotiana,* here also is the rule. So far as present evidence indicates this characteristic is rather strictly confined in *Nicotiana* to the variety "Cuba." This behavior of recessive factors of *Tabacum* varieties in hybrids with *sylvestris* is a striking confirmation of the conception that in such cases there is a contrast between distinct reaction systems rather than between certain factors as opposed to each other. In general when *Tabacum* varieties of the type mentioned above are crossed with each other the hybrids, especially with respect to flower color, leaf shape, etc., are intermediate. The contrast in this case is not one between two distinct Mendelian reaction systems, but it is merely a contrast of certain differences within a common system, and the segregation in subsequent generations, although complex, indicates a general accordance with normal Mendelian expectation. But in the case of species hybrids between *Tabacum* and *sylvestris* the contrast is between distinct

Mendelian reaction systems and the consistent reproduction of all *Tabacum* characters, whether qualitative or quantitative, indicates at one and the same time that these are fundamentally of the same nature, depending essentially for their expression on a complex set of Mendelian factors, and, moreover, that the *Tabacum* system as a unit dominates the course of somatogenesis and determines the reaction end products of the two systems.

This domination of the somatogenic processes by the *Tabacum* reaction system is followed by important experimental possibilities. If the species hybrids always display the *Tabacum* characteristics as completely as all our present evidence indicates that they do, then they will furnish a powerful method of attack on the problem of Mendelian behavior in the *Tabacum* section of the genus *Nicotiana*. For by crossing hybrids between *Tabacum* varieties with *sylvestris*, it should be possible to secure in the partially sterile hybrids resulting a phenotypic reproduction of the gametic series of the *Tabacum* parent. This series would not be complicated by intergrading of heterozygous forms, because the plants thus obtained would exhibit the phenotypic characters of homozygotes, and recessive factors as well as dominant ones would be reproduced in their proper place in the *Tabacum* system. Apparently it should be possible, therefore, to demonstrate the fundamentally similar nature of linkage in *Nicotiana* and *Drosophila*. Such an analysis will still be very difficult in *Nicotiana* on account of its high chromosome number, but by the method of procedure outlined above some distinct advance at least seems perfectly feasible. These, however, are matters on which we have as yet very little data.

Since, therefore, the *Tabacum* reaction system dominates the somatogenic processes in the hybrid to nearly or quite the exclusion of the *sylvestris* system, the elements of the two systems must be largely mutually incompatible. Free interchanges between the two systems would not, therefore, necessarily result in the formation

of functional Mendelian reaction systems. This high degree of mutual incompatibility of the two reaction systems exhibits itself in the high degree of sterility of the F_1 hybrids. As Goodspeed (1912, *l. c.*) has shown, however, this sterility is only partial and a few good ovules are formed which produce viable seed in the case of open pollination or when crossed back with the parents. In evidence which is presented elsewhere (Goodspeed and Ayres, 1916) it has been shown that, while it is experimentally possible to modify the behavior of the F_1 plants in such a manner that the fruits without pollination are retained for a considerable period rather than falling soon after anthesis, the percentage of good ovules produced can not be appreciably modified. This is an important point, for it indicates that the number of good ovules produced is a function of the chromatin behavior and not to be influenced by environmental factors, and that they should, therefore, exhibit a consistent behavior and lend themselves to a logical interpretation. In fact, evidence at hand indicates that the small percentage of functional ovules represents the *Tabacum* and *sylvestris* extremes of a recombination series, and that, therefore, the middle members of the series, which are made up of relatively high proportions of both *Tabacum* and *sylvestris* elements, fail to function because they produce incompatible reaction systems. This is shown clearly by back crosses which have been made with the parents, although here portions of our evidence are not so well controlled as we would prefer. When back crosses are made with *sylvestris* as the pollen parent there is produced a variety of forms many of which are highly abnormal, but among them there is a considerable proportion of plants which are pure *sylvestris* in all characters. These plants are fertile and have bred true to the *sylvestris* type for three generations. A number of the remaining plants resemble *sylvestris*, but show contamination with other elements presumably derived from the *Taba-*

cum reaction system. These contaminations affect the whole plant, not alone any particular character complex. All plants except those which were of the pure *sylvestris* type were sterile. Until this year we have not been able to secure seed from back crosses with the *Tabacum* parent, but from open pollinated seed a variety of forms is produced, practically all of which are of the *Tabacum* type in general appearance. This result is evidently due to pollination of the F_1 flowers with pollen from the wide series of *Tabacum* forms which, in predominating numbers, have always been grown in the cultures. Some of these plants resulting from uncontrolled pollination were likewise fertile. They have been grown for several generations and although displaying segregation, this segregation has never involved the production of *sylvestris* characters, but has been of a type normally found within varietal hybrids of *Tabacum*. The sterile forms in this series largely resembled the F_1 hybrids of *Tabacum* and *sylvestris*, and the occurrence of a few aberrant and *sylvestris* forms which were obtained from the sowing of the open pollinated seed are what would be expected, if pollination was sometimes effected with *sylvestris* pollen.

It appears, therefore, that for these species hybrids the conception of the factors as making up for each species a reaction system in which the elements have a specific relation to one another harmonizes the results obtained with the more recent Mendelian developments. The objection which might be made that interchanges of factors which behave normally in one system should not logically be followed by such profound disturbances as to completely prevent the formation of a functional reaction system is met by several counter considerations. In the discussion of lethal factors it has been pointed out that Morgan (1914, *l. c.*) has demonstrated that changes in many loci of the *Drosophila* system have been followed by failure of the resulting individual to develop. It is entirely conceivable that, if a certain factor *A* in one system

be considered, the corresponding factor *A'* in the other system, if there be such a factor, might be just as different from *A* as a lethal factor is different from its normal allelomorph. Further, from a modern Mendelian viewpoint there is no basis for assuming that recombinations could be obtained involving only exchanges in isolated loci in the systems. For if the behavior in segregation in the F_1 hybrids corresponds to that in *Drosophila* then such combinations as could be obtained would depend on the shifting of entire choromosomes or in case of crossing-over of relatively large portions of chromosomes. The recombinations obtained in the hybrids between *Tabacum* varieties and *sylvestris,* provided chromosome distribution takes place after the normal fashion in these hybrids, would involve, therefore, for the most part, the formation of systems containing either whole chromosomes or large sections of chromosomes of opposing systems. Such attempted reconstruction of systems might well fail in cases of any marked specificity in the relations of the factors of the opposing reaction systems, since any large proportions of both systems in a gamete might conceivably destroy the continuity or the balanced relations necessary for the continuance of system reactions. When the proportions of one or the other system are relatively small, the system reactions might be merely disturbed, resulting in the production of the abnormal forms which have been secured in our cultures. It is to such relations between the two systems involved that we ascribe the selective elimination of the greater portion of the possible gametic combinations in the crosses between *Tabacum* varieties and *sylvestris,* and which, therefore, results in a high degree of sterility in these hybrids.

It is of course obvious that there are many categories of sterility, in the hereditary sense as well as in the physiological sense. The particular type herein considered is that which results from relatively wide crossing such as is involved in species hybrids. That certain types of steril-

ity are due to specific factors which display consistent Mendelian behavior has been demonstrated by Bateson and Punnett (1908) and others and has been suggested by Correns (1913) for cases which are concerned with the specific category of normal self-sterility in *Cardamine pratensis*. It appears, nevertheless, as East (1915) in principle has suggested, that many cases in which sterility has followed rather wide crossing would seem to be susceptible of a more logical treatment from the standpoint of non-specific disturbances in the reaction systems involved.

(*To be continued*)

COMPARATIVE RESISTANCE OF PRUNUS TO CROWN GALL[1]

PROFESSOR CLAYTON O. SMITH

UNIVERSITY OF CALIFORNIA

IN making a study of the plant disease popularly known as crown gall, plant tumor, or plant cancer, it seemed desirable to ascertain the relative resistance of the different species of *Prunus* to this disease. It was soon evident that the usual methods employed in discovering disease resistance would be of little value. The cause of the disease, life history and pathogenic nature of the organism had already been studied by Dr. Erwin F. Smith[2] and his assistants of the United States Department of Agriculture. They showed, by artificial inoculations, the wide range of plants susceptible to infection and also found that some were apparently resistant. Their experiments encouraged the writer to follow with slight modifications the method of artificial inoculations on a number of species and varieties of the genus *Prunus*. It was hoped that suitable resistant stock might be discovered that would be adapted to the propagation of the stone fruits.

Before considering in detail the methods employed, the general characteristics of the disease will be briefly given. The affected part of the tree, shrub or plant is generally found a little distance beneath the surface of the soil at the crown or point where the roots are given off from the trunk. The disease is characterized by an enlargement or gall more or less spherical in shape and consisting of tissue that is usually much softer in texture than normal. The surface may or may not be covered with a normal bark. This enlargement is now known to be caused by a stimulus that comes from the presence of a definite motile bacterial organism known as *Bacterium* (*Pseudomonas*) *tumefaciens*, which lives within certain of the plant cells in relatively small numbers.

Considerable attention was given to perfecting methods for

[1] Paper No. 28, Citrus Experiment Station, College of Agriculture, University of California, Riverside, California.

[2] United States Department of Agriculture, Bureau of Plant Industry, Bulletins No. 213 and 255, 1911, 1912.

the determination of the relative resistance of the different species of *Prunus*. Most of the different species and varieties were budded or grafted on other stock, the scions or bud wood being secured from several reliable sources, such as the Arnold Arboretum, several of the larger nurseries. The methods used are somewhat different from those usually employed in seeking for disease resistance among plants. The plan was to artificially inoculate with pure virulent laboratory cultures the different kind of *Prunus* under experimentation. A number of suscep-

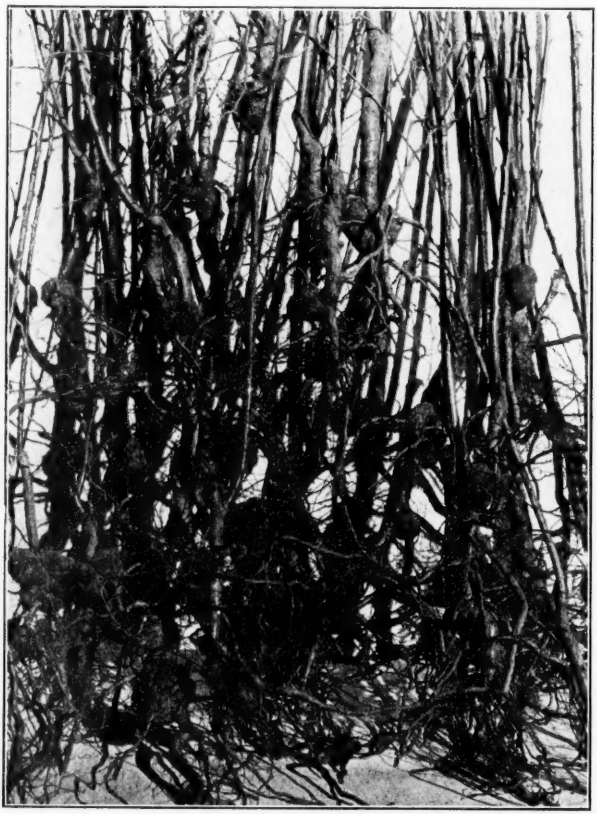


FIG. 1. A bunch of galled peach stock as they often occur in the nursery. Many of the other trees probably had incipient infections unrecognizable at the time of digging, which later developed galls.

tible hosts were always included in the experiment, to act as a check upon the virulence of the culture and any unfavorable climatic condition. In each series of inoculation 5 or 10 punctures were made upon vigorous growing twigs of the current

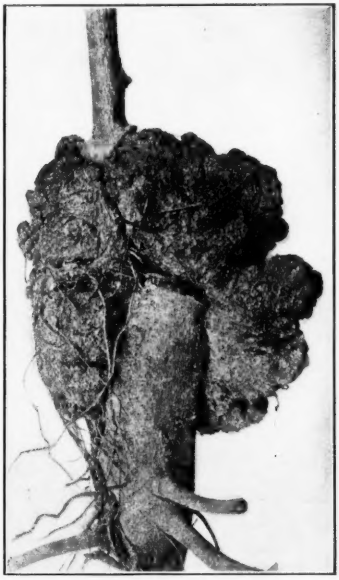


FIG. 2. Natural gall on English walnut in nursery. This gall appeared at the point where the English walnut stock was grafted. It is common practice to bank the dirt about the scions to prevent drying. The California black root is much more resistant.

year's growth. During the experiments of 1914, ten punctures were always made. This number, being the same in all the experiments, was of material aid in the final compilation of results. Other check punctures were made in the same way as in the inoculations except that none of the organisms were placed in the tissue. An ordinary steel needle in a cedar handle was used in making the puncture inoculations. This was first flamed, then used to convey some of the bacterial growth from the test tube to the twig to be inoculated, the puncture being made through the bark and wood of twig. The organism was grown in a medium made as follows: $\frac{1}{2}$ per cent. glucose, $\frac{1}{2}$ per cent. sodium chloride, $\frac{1}{2}$ per cent. meat extract, 1 per cent. peptone, 1 per cent. agar.

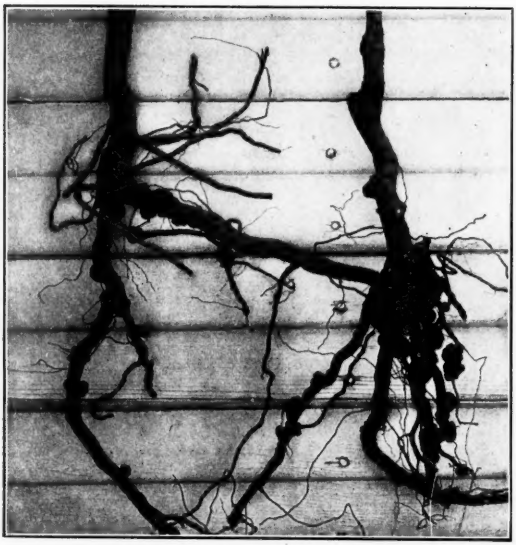


FIG. 3. Two almond roots naturally infected with numerous galls. Such stock would only make inferior trees.

The tubes were incubated from twenty-four to thirty-six hours before being used, at which time there was a vigorous, pearly white, raised growth where the medium was inoculated. The series of inoculations were made a week apart from May 1 to about September 1, 1914. The work of 1913, while similar in nature, was not so extensive as that of 1914. The experiments thus extended over the period of the year when the trees are making their most rapid growth, and should be in their most susceptible condition for infection. The trees were well cared for and made rapid growth during the period the experiments were in progress, and hence were in favorable condition for the development of the disease. No effort was made to protect in any way the punctures, as the use of wax or other covering stimulates callus formation which could easily be confused with the beginning stages of a young gall or with one that has not matured rapidly, as is often the case on inoculated trees showing resistance.

The genus *Prunus* gives a wide range for investigation because of the large number of species and varieties. The following are the species thus far tested by artificial inoculations:

Prunus Allegheniensis, P. Americana, P. Amygdalus, P. andersonii, P. Armeniaca, P. Armeniaca, var. Mikado, *P. Avium, P. Besseyi, P. Caroliniana, P. cerasifera, P. cerasifera,* var. *divaricata, P. cerasifera,* var. *Planteriensis, P. domestica,* several different varieties, *P. eriogyna, P. glandulosa, P. hortulana, P. ilicifolia, P. integrifolia, P. Japonica, P. maritima, P. Mahaleb, P. Mitis, P. monticola, P. Mume, P. munsoniana, P. nigra, P. orthosepala, P. Pennsylvanica, P. Persica,* several varieties, *P. platycarpa, P. pumila* (Linn.), *P. serotina, P. Simonii, P. Watsoni.*

All the above hosts gave positive results from artificial inoculation, except *P. pumila, P. ilicifolia* and *P. Caroliniana.* These three hosts were inoculated during 1913 and 1914 and have always showed negative results. *P. ilicifolia* and *P. Caroliniana* were on their own roots and were not making very rapid growth at the time of the experiment, but it seems almost impossible that they should not have been in a susceptible condition some time during the period from May to September. *P. pumila* made rapid growth, as it was grafted on peach stock, but never showed the least indication of gall formation, nor has it during the ex-

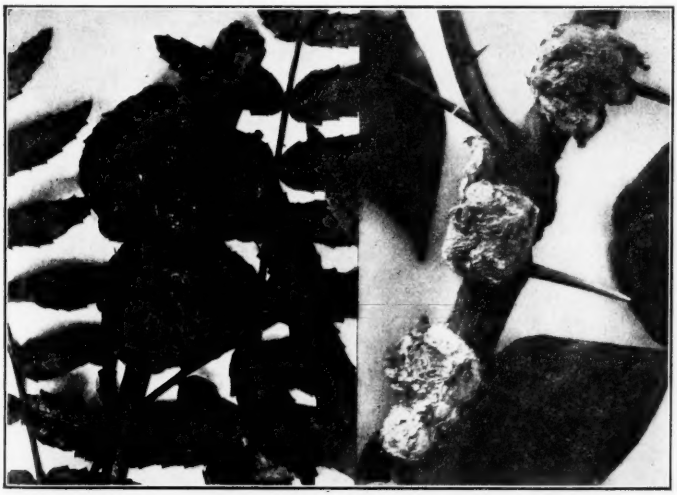


FIG. 4. FIG. 5.

FIG. 4. Artificial gall produced on pepper tree, *Schinus Molle.*

FIG. 5. Artificial gall made by inoculating sour orange seedlings. Citrus stock is only rarely infected naturally with gall, but galls have been artificially produced on lime, lemon, orange and shaddock.

periments of 1915. Only a part of the kinds of *Prunus* just mentioned were thoroughly tested out and these only are included in tabulated results.

It will be noted that Tables II and III represent two varieties of *Prunus domestica.* Not all varieties, however, are equally resistant, but, in general, members of this group are much more

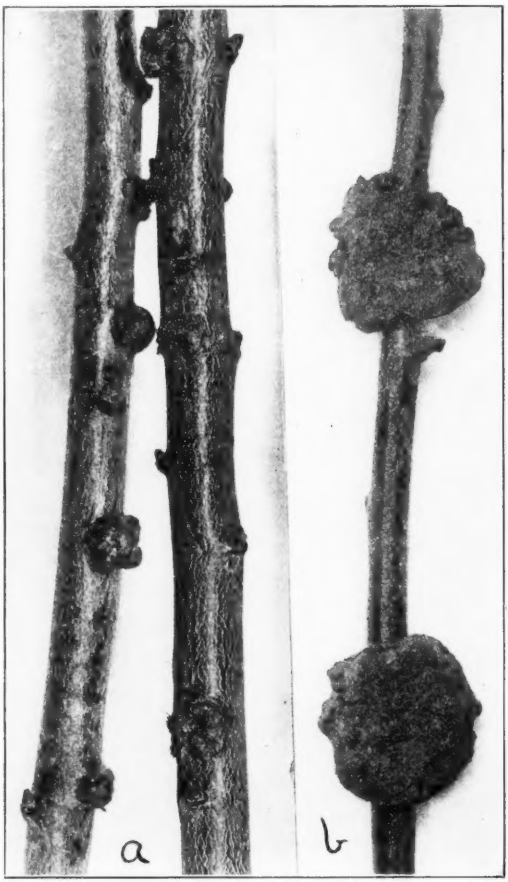


FIG. 6. Artificial galls on *Prunus.* (*a*) German prune, *P. domestica,* a resistant variety. (*b*) Myrobolan, *P. cerasifera,* a susceptible species. Note the difference in size of galls and how in the susceptible kind the galls eventually surround the twig.

TABLE I

A TYPICAL EXPERIMENT WITH *Bacterium tumefaciens*, CULTURE NO. 753 C (JULY 13 TO NOVEMBER 15, 1914), TO ILLUSTRATE GENERAL METHODS USED IN SEARCHING FOR A RESISTANT STOCK. A SIMILAR EXPERIMENT TO THIS WAS MADE EACH WEEK FROM MAY TO SEPTEMBER, 1914.

Experiment 20

Experiment Serial No.	No. of Inoculations	Positive Inoculations	Host	Size of Galls in Inches
745	10	2	German prune	$\frac{1}{8}$–$\frac{1}{4}$
746	10	0	German prune (old)	
747	10	5	Damson	$\frac{1}{16}$–$\frac{1}{8}$
748	10	10	*P. triflora*	$\frac{1}{16}$–$\frac{1}{2}$
749	10	10	Wickson	$\frac{3}{8}$–$\frac{3}{4}$
750	10	9	Burbank	$\frac{1}{2}$–$\frac{3}{4}$
751	10	10	Myrobolan	$\frac{1}{2}$–$\frac{3}{4}$
752	10	10	*P. Munsoniana*	$\frac{1}{4}$–$\frac{3}{8}$
753	10	10	*P. davidiana*	$\frac{1}{4}$–$\frac{1}{2}$
754	10	5	*P. maritima*	$\frac{1}{16}$–$\frac{1}{4}$
755	10	4	*P. dasycarpa*	$\frac{1}{16}$–$\frac{1}{8}$
756	10	0	Golden drop (silver prune)	
757	10	8	Reine Claude (green gage)	$\frac{1}{16}$–$\frac{3}{8}$
758	10	10	*P. Simonii*	$\frac{1}{4}$–$\frac{1}{2}$
759	10	10	Royal apricot	$\frac{1}{4}$–$\frac{1}{2}$
760	10	10	Elberta peach	1–1$\frac{1}{4}$
761	10	0	Bitter almond	
762	10	9	*P. hortulana*	$\frac{1}{4}$–$\frac{3}{8}$
763	10	5	*P. Americana*	$\frac{1}{16}$–$\frac{1}{8}$
764	10	10	*Schinus Molle*	1–1$\frac{1}{2}$
765	10	Positive	Oleander	
766	10	0	*P. pumila*	
767	10	0	*P. Watsoni*	
768	10	8	*P. nigra*	$\frac{1}{4}$–$\frac{1}{2}$
769	10	3	*P. serotina*	$\frac{1}{16}$–$\frac{1}{8}$
770	10	10	*P. institia pendula*	$\frac{1}{2}$–$\frac{3}{4}$
771	10	9	*P. mitis*	$\frac{1}{16}$ small
772	10	10	*P. Mume*	$\frac{1}{2}$–$\frac{3}{4}$
773	10	7	*P. Andersonii*	$\frac{1}{4}$
774	10	6	Duane (Tribble)	$\frac{1}{8}$–$\frac{3}{8}$
775	10	2	*P. Planteriensis*	$\frac{1}{16}$–$\frac{1}{8}$
776	10	8	Myrobolan (Arnold)	$\frac{1}{16}$–$\frac{1}{4}$
77	10	9	Myrobolan (sprouts)	$\frac{3}{4}$–1
778	10	10	Myrobolan (young sprouts)	$\frac{1}{2}$–$\frac{3}{4}$
779	10	10	El Paso	$\frac{1}{2}$–$\frac{3}{4}$
780	10	0	Golden beauty	
781	10	10	Arkansas	$\frac{1}{8}$–$\frac{1}{4}$
782	10	1	*P. Virginiana*	$\frac{3}{16}$
783	10	7	*P. cerasifera divarica*	$\frac{1}{2}$–$\frac{3}{4}$
784	10	2	*P. Besseyi*	$\frac{1}{16}$
785	10	0	*P. ilicifolia*	
786	10	0	*P. Caroliniana*	
787	10	9	*P. orthosepala*	$\frac{1}{4}$–$\frac{1}{8}$
788	10	0	Olive	
789	10	2	*P. Armeniaca* Mikado	$\frac{1}{8}$–$\frac{1}{2}$
790	10	5	Italian prune	$\frac{1}{16}$–$\frac{1}{8}$

so than most other species of the genus. By comparison with other tables, it will be found that the galls are of a much smaller size than on most other hosts. The number of positive inocula-

TABLE II

SUMMARY OF ARTIFICIAL INOCULATIONS ON GERMAN PRUNE, *Prunus domestica*. CONCLUDED NOVEMBER 15, 1914

Experiment Serial No.	Date	No. of Inoculations	Positive Inoculations	Size of Galls in Inches
x 500[3]	5/ 3/14	10	0	
532	5/25/14	10	0	
559	6/18/14	10	0	
x 560	6/18/14	10	0	
617	6/29/14	10	6	$\frac{1}{8}$–$\frac{1}{4}$
x 618	6/29/14	20	0	
667	6/29/14	Check	0	
679	7/ 6/14	10	6	$\frac{1}{8}$–$\frac{1}{4}$
x 680	7/ 6/14	10	0	
745	7/13/14	10	2	$\frac{1}{8}$–$\frac{1}{4}$
x 746	7/13/14	10	0	
x 792	7/20/14	10	0	
870	7/27/14	10	0	
x 871	7/27/14	10	0	
934	8/ 3/14	Check	0	
x 935	8/ 3/14	Check	0	
995	8/ 4/14	10	2	$\frac{1}{8}$–$\frac{3}{16}$
x 996	8/ 4/14	10	0	
A 15	8/10/14	10	0	
A 87	8/15/14	10	0	
xA 88	8/15/14	10	0	
*A*125	8/17/14	10	0	
*A*207	8/24/14	10	8	$\frac{3}{16}$–$\frac{1}{16}$
*xA*208	8/24/14	10	0	
*A*242	8/31/14	10	0	
*xA*243	8/31/14	10	0	
		240	24	

tions as given in Tables II and III, is probably somewhat greater than it should be, as in making the estimate of the number of galls on these resistant stocks, any small enlargement was counted, and subsequent examination has shown that many of these small enlargements have not further increased in size. When a gall becomes established in a resistant variety, it makes rapid growth and eventually forms one of good size. These large galls differ from similar galls on peach and many other hosts in that the gall is attached to a relatively small circumference of the infected twig. The gall growth is often nearly at

[3] Numbers that are preceded by an *x* were made on rapid growing twigs of the current year of a seven-year-old tree. The other inoculations in a young tree two years old from the nursery.

TABLE III

SUMMARY OF ARTIFICIAL INOCULATIONS ON ITALIAN PRUNE (FELLENBERG) *Prunus domestica.* CONCLUDED NOVEMBER, 1913

Experiment Serial No.	Date	No. of Inoculations	Positive Inoculations	Size of Galls in Inches
211	5/10/13	5	0	
216	6/ 1/13	5	2	$\frac{4}{16}$–$\frac{1}{16}$
252	6/13/13	5	0	
264	6/16/13	5	0	
270	6/17/13	5	0	
282	7/14/13	15	5	$\frac{2}{16}$–$\frac{2}{16}$–$\frac{3}{16}$–$\frac{4}{16}$–$\frac{8}{16}$
292	7/13/13	5	0	
315	7/19/13	6	2	$\frac{2}{16}$–$\frac{4}{16}$
328	7/21/13	6	1	$\frac{2}{16}$
332	7/21/13	5	0	
343	7/22/13	5	0	
355	7/25/13	10	4	$\frac{1}{16}$–$\frac{3}{16}$–$\frac{2}{16}$–$\frac{1}{16}$
366	7/30/13	10	0	
259	6/ 9/13	5	0	
375	7/30/13	10	0	
390	8/ 9/13	10	0	
406	8/14/13	10	3	$\frac{2}{16}$–$\frac{1}{16}$–$\frac{1}{16}$
420	8/14/13	5	0	
		127	17	

right angles to the twig which makes these galls stand out for considerable distance from the branch.

It is of interest to note that both of these are prunes that have been under cultivation for many years. The German prune is described as being one of the plums longest under cultivation and the oldest of the prune type. Seedlings also come reasonably true to type which might be of importance if grown from seed for a stock. The Italian prune (Fellenberg) is the popular prune of Oregon and has a history of over a century's cultivation. Further experiments among varieties of the *domestica* group are being carried on. The damson which is sometimes included among the domesticas, shows considerable resistance to artificial inoculation.

Prunus cerasifera, var. *Planteriensis,* Table VIII, is described as a double flowering shrub and is the most gall resistant of any of the tested varieties of *cerasifera,* although this resistance should be again determined. Inoculations in the Arnold Arboretum trees, Table IV, did not develop as many galls as those of the larger Myrobolan tree, either because the former were not

[4] A local commercial stock, propagated in California from sprouts, not the true Duane variety, but a small blue plum having the flavor of a Damson, but differing in shape.

TABLE IV

SUMMARY OF ARTIFICIAL INOCULATIONS ON *Prunus cerasifera*. CONCLUDED NOVEMBER, 1914

Prunus cerasifera, Arnold Arboretum Type

Experiment Serial No.	Date	No. of Inoculations	Positive Inoculations	Size of Galls in Inches
595	6/20/14	10	10	$\frac{1}{4}$–$\frac{1}{2}$
646	6/29/14	10	8	$\frac{1}{16}$–$\frac{3}{16}$
709	7 6/14	10	9	$\frac{1}{16}$–$\frac{1}{8}$
776	7/13/14	10	8	$\frac{1}{16}$–$\frac{1}{4}$
22	7/20/14	10	5	$\frac{1}{16}$
902	7/27/14	10	8	$\frac{1}{8}$–$\frac{1}{4}$
963	8/ 3/14	Check	0	
A 1	8/10/14	10	4	$\frac{1}{4}$–$\frac{1}{8}$
*A*111	8/15/14	10	2	$\frac{1}{16}$
*A*149	8/17/14	10	4	$\frac{1}{16}$
*A*225	8/24/14	10	10	$\frac{1}{16}$–
*A*253	8/31/14	10	2	$\frac{1}{16}$
		110	70	

Prunus cerasifera (large four year old seedling).

Experiment Serial No.	Date	No. of Inoculations	Positive Inoculations	Size of Galls in Inches
506	5/ 5/14	10	10	$1\frac{1}{4}$–$1\frac{1}{2}$
538	5/25/14	10	10	$\frac{1}{4}$–$\frac{1}{2}$
566	6/18/14	10	10	$\frac{1}{2}$–$\frac{3}{4}$
6?	6/29/14	10	10	$\frac{1}{2}$–$\frac{3}{4}$
649	6/29/14	10	10	$\frac{3}{4}$–1
686	7/ 6/14	10	10	$\frac{1}{4}$–$\frac{1}{2}$
751	7/13/14	10	10	$\frac{1}{2}$–$\frac{3}{4}$
821	7/20/14	10	10	$\frac{1}{2}$–$\frac{3}{4}$
901	7/27/14	10	10	$\frac{1}{8}$–$\frac{3}{4}$
962	8/ 3/14	Check	0	
A 9	8/ 4/14	10	10	$\frac{1}{2}$–$\frac{3}{4}$
A 40	8/10/14	10	10	$\frac{1}{4}$–$\frac{1}{2}$
*A*110	8/15/14	10	10	$\frac{1}{2}$–$\frac{3}{4}$
*A*148	8/17/14	1	10	$\frac{1}{4}$–$\frac{1}{2}$
*A*214	8/24/14	10	10	$\frac{1}{4}$–$\frac{1}{2}$
*A*251	8/31/14	10	10	
		150	150	

growing as rapidly, or, judging from their shrub-like growth, because they are of a different type possibly nearer to the wild type than are those commonly imported from France by nurserymen.

The variety known as Golden Beauty, *P. hortulana*, has thus far shown more marked resistance than other varieties of the species thus far tested. It is interesting to remember that this variety is supposed to have originated in western Texas some-

what out of the natural range of the species. *P. hortulana* and *P. americana* are used as a stock for the native plums in the middle west and east. *P. hortulana* does not sucker, fruits abundantly and has a number of excellent qualities that would recommend it as a stock. Further experiments with varieties of this species are being made and its adaptability to various of our stone fruits carefully studied.

TABLE V

SUMMARY OF ARTIFICIAL INOCULATIONS ON GOLDEN BEAUTY, *Prunus hortulana*. CONCLUDED NOVEMBER, 1914

Experiment Serial No.	Date	No. of Inoculations	Positive Inoculations	Size of Galls in Inches
600	6/20/14	10	7	$\frac{1}{16}$
651	6/29/14	10	3	$\frac{1}{16}$ very small
714	7/ 6/14	10	5	$\frac{1}{16}$–$\frac{1}{8}$
780	7/13/14	10	0	
826	7/20/14	10	4	$\frac{1}{16}$
906	7/27/14	10	1	$\frac{1}{16}$
967	8/ 3/14	Check	0	
A 11	8/ 4/14	10	3	$\frac{1}{8}$
A 44	8/10/14	10		
*A*114	8/15/14	10	1	$\frac{1}{16}$
*A*152	8/17/14	10	1	$\frac{1}{16}$
*A*250	8/29/14	10	0	
		110	25	

TABLE VI

SUMMARY OF ARTIFICIAL INOCULATIONS ON *Prunus pumila* LINN. CONCLUDED NOVEMBER 15, 1914

Experiment Serial No.	Date	No. of Inoculations	Positive Inoculations
580	6/20/14	10	0
635	6/29/14	10	0
766	7/13/14	10	0
849	7/20/14	10	0
88	7/27/14	10	0
9 4	8/ 3/14	Check	0
A 8	8/ 4/14	10	0
A 34	8/10/14	10	0
*A*106	8/15/14	10	0
*A*144	8/17/14	10	0
*A*220	8/24/14	10	0
*A*254	8/31/14	10	0
		110	

Further inoculations of *P. pumila* (thirteen experiments of ten inoculations each or 130) made during the present year, 1915,

in vigorous growing seedlings, gave negative results, agreeing with the results of the two previous years. The experiments thus far conducted show that the species is entirely resistant to artificial inoculations. *P. Besseyi,* closely related to *P. pumila,* also shows considerable resistance.

The two other species of *Prunus* referred to as being resistant are *P. ilicifolia* and *P. Caroliniana.* They are evergreens and are not now considered as strictly belonging to the genus *Prunus.* They do not readily unite by grafting or budding with varieties of the stone fruits. *P. pumila* is a shrub and while this stock readily unites with many of the varieties of the stone fruits it probably would dwarf the tree more or less and might sprout. It is, however, readily grown from pits or cuttings.

TABLE VII

SUMMARY OF ARTIFICIAL INOCULATIONS ON *Prunus.* CONCLUDED OCTOBER 31, 1913

Species	Variety	No. of Inoculations	Positive Inoculations	Per Cent.	Size of Galls in Inches
P. domestica	German prune	75	2	$2\frac{2}{3}$	$\frac{1}{16}$–$\frac{1}{8}$
P. domestica	German prune	50	5	10	$\frac{1}{10}$–$\frac{1}{8}$
P. domestica	Italian prune	127	17	13	$\frac{1}{16}$–$\frac{1}{4}$
P. domestica	Green gage	17	4	23	$\frac{1}{16}$–$\frac{3}{8}$
P. insititia	Damson	138	51	37	$\frac{1}{4}$–$\frac{3}{4}$
P. domestica	Duane	37	15	40	
P. persica	Elberta	61	57	93	$\frac{1}{2}$–$2\frac{1}{2}$
P. triflora × *P. Simonii*	Wickson (hybrid)	56	64	98	$\frac{1}{2}$–1
P. triflora	Burbank	31	31	100	$\frac{1}{4}$–$\frac{1}{2}$
P. cerasifera	Myrobolan	8	8	100	$\frac{1}{2}$–1

In each of the inoculation experiments, ten punctures were made, hence the number of inoculations divided by ten will give the number of separate experiments made with the various hosts.

In the two tables, VII and VIII, where the inoculations of the years 1913 and 1914 have been summarized, there is a reasonable degree of consistency between the percentages shown for the different hosts. Other varieties of *P. persica* possibly should be further tested, although such varieties as Elberta, Saucer or Peento, Salway, Lovell and Muir seedlings have not shown any marked resistance.

Any of the stock as listed in Tables VII and VIII that show less than 50 per cent. infection are more or less promising, for in the experimental work with artificial inoculations from virulent

TABLE VIII

SUMMARY OF INOCULATIONS MADE ON *Prunus*. CONCLUDED NOVEMBER 15, 1914

Species	Variety	No. of Inoculations	Positive Inoculations	Per Cent. of Galls	Size of Galls in Inches[5]
P. pumila	2 varieties, Arnold Arboretum	110	0	0	
P. domestica	Italian prune	140	10	7	$\frac{1}{16}$–$\frac{1}{8}$
P. cerasifera	*P. planteriensis*	40	3	$7\frac{1}{2}$	$\frac{1}{16}$–$\frac{1}{8}$
P. domestica	German prune	240	24	10	$\frac{1}{16}$–$\frac{1}{2}$
P. insititia	Damson	120	13	10	$\frac{1}{8}$–$\frac{1}{2}$
P. Besseyi	———	50	5	10	$\frac{1}{8}$–$\frac{1}{2}$
P. hortulana	Golden Beauty	110	25	22	$\frac{1}{16}$–$\frac{1}{8}$
P. amygdalus[4]	Bitter almond	100	22	25	$\frac{1}{8}$–$\frac{3}{8}$
P. domestica	Reine Claude (green gage)	90	25	26	$\frac{1}{16}$–$\frac{1}{2}$
P. Armeniaca	Mikado	40	11	27	$\frac{1}{16}$–$\frac{3}{16}$
P. angustifolia	Watsoni	50	15	30	$\frac{1}{16}$–$\frac{1}{8}$
P. maritima	Arnold Arboretum	140	48	34	$\frac{1}{16}$–$\frac{3}{8}$
P. dasycarpa	Arnold Arboretum	130	55	42	$\frac{1}{16}$–$\frac{1}{2}$
P. Mitis	Arnold Arboretum	60	32	53	$\frac{1}{16}$–$\frac{1}{8}$
P. cerasifera	Arnold Arboretum	110	70	63	$\frac{1}{16}$–$\frac{1}{4}$
P. Munsoniana	Arnold Arboretum	70	48	68	$\frac{1}{8}$–$\frac{3}{16}$
P. Munsoniana	Arkansas	90	70	77	$\frac{1}{16}$–$\frac{3}{8}$
P. Americana	Arnold Arboretum	100	83	83	$\frac{1}{16}$–$\frac{1}{2}$
P. hortulana	Arnold Arboretum	130	108	83	$\frac{1}{8}$–$\frac{3}{4}$
P. insititia	Pendula	90	77	85	$\frac{1}{16}$–$\frac{3}{4}$
P. davidiana	———	110	96	88	$\frac{1}{8}$–$\frac{3}{4}$
Schinus Molle	Pepper tree	110	97	88	$\frac{1}{4}$–$1\frac{1}{2}$
P. triflora	Burbank	120	109	90	$\frac{1}{2}$–$1\frac{1}{2}$
P. nigra	Arnold Arboretum	60	56	90	$\frac{1}{4}$–$\frac{3}{8}$
P. orthosepala	Arnold Arboretum	80	72	90	$\frac{1}{16}$–$\frac{1}{8}$
P. Mume	Arnold Arboretum	100	91	91	$\frac{1}{4}$–$\frac{1}{2}$
P. Munsoniana	Pits Arnold	140	130	92	$\frac{1}{16}$–$1\frac{1}{2}$
P. cerasifera	*P. divaricata*	100	94	94	$\frac{1}{8}$–$\frac{3}{4}$
P. Persica	Elberta	130	122	94	$\frac{1}{4}$–$\frac{3}{4}$
P. Armenica	Royal apricot	120	117	97	$\frac{1}{4}$–1
P. triflora	Arnold Arboretum	140	137	97	$\frac{1}{8}$–$\frac{3}{4}$
P. Munsoniana	El Paso	100	97	97	$\frac{1}{4}$–$\frac{1}{2}$
P. cerasifera	Sprouts	120	117	97	$\frac{1}{4}$–$1\frac{1}{2}$
P. triflora × *P. Simonii*	Wickson (hybrid)	140	138	98	$\frac{1}{8}$–$\frac{3}{4}$
P. cerasifera	Tree	150	150	100	$\frac{1}{4}$–$1\frac{1}{2}$
P. monticola	Arizona Experiment Sta.	40	40	100	$\frac{1}{2}$–$1\frac{1}{2}$
P. Simonii	Arnold Arboretum	130	130	100	$\frac{1}{4}$–$1\frac{1}{2}$

cultures, the different stocks were subject to a more severe test than obtains under the usual field conditions. The more promising of these, the first seven in Table VIII, with the exception of the damson, have already been considered after the various table in which the results were summarized. The damson has often

[5] *Prunus Amygdalus* was not growing well during the last part of the season and no infections showed after that of July 6. Before this time a large percentage of the inoculations were positive. This will be repeated another year.

been used as a stock, but is not popular on the Pacific coast because of its slow growth in the nursery and the difficulty of working it with many of the stone fruits. Duane, *P. domestica,* Table VII, is being used to some extent as a stock in California and shows resistance to gall in old vineyard land where it has been grown for six years. It makes as large a tree as the popular Myrobolan stock. The seedlings are grown from suckers, which give a root likely to sucker. Reine Claude (green gage) variety has shown resistance and would without doubt be a good stock for the domestic type of plums. *P. Armeniaca,* variety Mikado, is an apricot that differs somewhat from the one commonly grown in California. It should be tested out experimentally as a stock for apricots to replace the susceptible one now being used.

The almond, from field observations, is one of our most susceptible stock and this is fully confirmed by the following inoculation experiments: Fourteen different varieties of almond seedlings not summarized in the following tables were inoculated in April of 1913 at the University Farm at Davis, California. These in all cases showed a high percentage of infection. So far the peaches and almonds have shown only slight resistance.

It will be noted that our most popular stocks as Myrobolan, peach, apricot and almond are very susceptible, which only goes to confirm field observations that the stock used for the stone fruits are very susceptible to crown gall.

The work so far conducted shows that seedlings of the German and Italian prunes might be promising stock for certain of the stone fruits, probably those of the *domestica* type. However, no definite recommendations can be given, as the work is now only in its preliminary stages.

SHORTER ARTICLES AND DISCUSSION

EUROPEAN FOSSIL FISH-SCALES

In European Cretaceous deposits fish-scales have been found at various times, and occasionally have been named and described by paleontologists. Dr. A. S. Woodward, in his great "Catalogue of the Fossil Fishes," has carefully and accurately listed all the names so given, but has made little or no attempt to examine the records critically, assuming that they were valueless, or nearly so. More recent work on fish-scales brings out the fact that these materials are of great value for the understanding of Mesozoic fish life, but unfortunately they have been described with little knowledge of their significant characters. An important pioneer work was that of Geinitz,[1] describing scales from the Turonian of Saxony. Geinitz realized that it was necessary to make comparisons with scales of recent fishes, and gave a plate of "Schuppen von lebenden Fischen," but unfortunately chose species which had little relationship, for the most part, with the fossils studied. The three plates of fossil scales appear to have been very carefully drawn, and from them it is possible to gather a number of facts not brought out in the text. *Cyclolepis agassizi* appears to be Salmonoid, agreeing quite well with the modern *Salmo*. *Aspidolepis steinlai* is like the scales of living Stromateidæ, as *Poronotus*. *Osmeroides divaricatus* evidently has nothing to do with the genus to which it is assigned, but is of characteristic Albulid type. *Osmeroides lewesiensis* (Mantell), as determined by Geinitz, consists in the main of scales agreeing with those of the remarkable living genus *Pterothrissus*. The genus *Cladocyclus* presents some serious difficulties. The type is a Brazilian species (*C. gardneri* Agassiz) from the Upper Cretaceous of the Province of Ceará. I am indebted to Dr. D. S. Jordan for material referred to this species, and it appears that the large scales have extremely fine circuli, while those of the lateral line possess branching canals of the same general type as those of the living S. American genus *Hydrolycus*.[2] It does not

[1] "Die Fossilen Fischschuppen aus dem Plänerkalke in Strehlen," 1868.

[2] These canals are in the *apical*, not the basal field, as erroneously stated by me in *Annals Carnegie Museum*, IX, p. 110.

seem certain that this is the true *Cladocyclus* of Agassiz; it may represent a new genus ancestral to the Neotropical Characoid fishes. European "*Cladocyclus*" is in any event surely distinct from the Brazilian. The *C. strehlensis* of Geinitz includes scales approaching those of *Potamalosa*, but the species is founded in the main on an entirely different type, which is evidently close to the English *C. lewesiensis*. It is a question what generic name should be used for the *lewesiensis-strehlensis* type, which must be removed from *Cladocyclus*. It was formerly included in *Hypsodon* Agassiz, but that generic name appears to belong properly to the fishes usually called *Portheus*, the type being *lewesiensis* Mantell = *mantelli* Newton. The name *lewesiensis* also belongs strictly to the *Portheus*, and the English so-called *Cladocyclus*, if distinct from the Geinitz species, seems to need a new name. These matters will be taken up more fully elsewhere at a later date. *Beryx ornatus* of Geinitz, properly called *Hoplopteryx lewesiensis* (Mantell), appears to be a primitive Berycoid type, having scales such as might be expected in an ancestor of the modern Berycidæ. *Hemilampronites steinlai* Geinitz consists of scales differing little from the living *Hyporhamphus*. The scales figured by Geinitz as those of *Macropoma mantelli* Agassiz[3] have no resemblance to that species; from the fine transverse circuli, basal radii, and apical teeth like those of *Pomacanthus*, they appear to belong to some Teleost more or less related to the Berycoids. Thus we find that although Geinitz knew little about the affinities of his scales, they had excellent characters, reminding us in certain cases of modern genera, and indicating the great antiquity and constancy of peculiarities of scale structure. In 1878 Anton Fritsch[4] undertook to describe the fish-scales of the Upper Cretaceous of Bohemia, and believed that he had a number of the species of Geinitz. His *Cladocyclus strehlensis* and *Cyclolepis agassizi* are perhaps correct, but the others are evidently different from the Geinitzian forms. His *Macropoma speciosum* Reuss is a genuine species of that genus, with quite characteristic scales. His *Macropoma forte*, on the other hand, appears to be a *Cœlacanthus*. His *Osmeroides lewesiensis* has regular transverse circuli between the radii, instead of the minute tubercles (markings like the surface of a strawberry) of the Geinitz scales

[3] *Macropoma mantelli* should be called *Macropoma lewesiensis* (Mantell), based on the *Amia(?) lewesiensis* of Mantell.

[4] "Die Reptilien und Fische der böhmischen Kreideformation."

and of *Pterothrissus*. His *O. divaricatus* is wholly distinct from the scale described by Geinitz under that name, and has not the Albulid characters. The *Beryx ornatus* scales are printed upside down, and the artist has added ctenoid structures (small teeth) above, on what is really the basal margin. In 1874 T. C. Winkler published a paper[5] in which he described two species from the scales. His *Osmeroides belgicus* appears to be congeneric with the *Osmeroides lewesiensis* as understood by Fritsch. His *Cycloides incisus*, supposed new genus and species, of which he says that he knows no fish, living or fossil, with such scales, is apparently worthless. It may not be a fish-scale. In America the fossil scales of Teleosts have received very little attention, but a large collection accumulated by the U. S. Geological Survey is now under review, and will undoubtedly yield much of value for the understanding of Mesozoic fishes, and at the same time throw light on the ancestry and relationships of modern families.

T. D. A. COCKERELL

UNIVERSITY OF COLORADO, BOULDER,
July 8, 1916

[5] "Mémoire sur quelques restes du Poissons du systéme heersien," *Arch. Mus. Teyler.*, IV.